

ON THE ORNITHISCHIAN DINOSAUR IGUANODON BERNISSARTENSIS FROM THE LOWER CRETACEOUS OF BERNISSART (BELGIUM)

A. — INTRODUCTION

An unexpected and spectacular discovery of fossil remains was made in the spring of 1878 at the small mining village of Bernissart, in South-West Belgium (fig. 1). The fossils were found in a broad, marl-filled fissure, which traversed a newly excavated gallery of the « Fosse Sainte Barbe » at the coal mine in Bernissart, some 322 metres below ground. The marls which were of Lower Cretaceous age, were found to contain a vast number of fossils, representing the principal elements of a flora and fauna which had flourished some 120 million years ago. Of all the remains that were discovered, perhaps the most renowned are the many complete, articulated skeletons of *Iguanodon*; their discovery marked the second of two significant phases of development in the study of dinosaurian reptiles, with which *Iguanodon* was quite closely linked.



FIG. 1. — An outline map of Belgium to illustrate the location of Bernissart.

Firstly, in 1841, Richard OWEN, in a report on British fossil reptiles to the British Association for the Advancement of Science, proposed that a new suborder of reptiles, the Dinosauria, be created to accommodate three recently discovered rather fragmentary fossil reptiles: *Megalosaurus* W. BUCKLAND (1924), *Iguanodon*

G.A. MANTELL (1825) and *Hylaeosaurus* G.A. MANTELL (1833). OWEN segregated these reptiles on the basis of several hitherto unnoticed anatomical peculiarities. The most notable of these were a sacrum composed of five fused vertebrae, and limb bones suggestive of animals with an upright stance. The failure to discover more adequate specimens of OWEN's dinosaurs for nearly four decades considerably hampered work on these enigmatic forms.

A further development toward a more clear understanding of the structure and relationships of dinosaurs was heralded by Joseph LEIDY (1858) with the description of *Hadrosaurus*, a more completely preserved animal from North America (New Jersey) which was comparable to *Iguanodon*. Somewhat later, Thomas HUXLEY published two papers (1868, 1870) on the structure and affinities of dinosaurs. However, it was not until 1878, with the discovery of complete dinosaur skeletons at Bernissart, that the intuitive work of HUXLEY could be verified. At about the same time that the discovery of dinosaurs was being made in Belgium, even more remarkable discoveries were made in North America; these led the way to a far better understanding of the nature of, and relationships between, dinosaurs. It seems fitting, therefore, that the first detailed study of the famous fossils from Bernissart, initiated during their centenary, should be commemorated in this Memoir.

This study constitutes a description of the anatomy and a discussion of some aspects of the biology of *Iguanodon bernissartensis*. This species is represented by a unique collection of twenty-four more or less complete, articulated skeletons, as well as several partly preserved individuals; these are all now in the collections of the Institut Royal des Sciences Naturelles de Belgique, Brussels. The majority of these specimens form a permanent display in the « Salle de l'ère Secondaire » of the Institut.

Since these dinosaurs have been the subject of a considerable number of scientific papers (twenty-four by Louis DOLLO alone), I feel obliged to offer a few words of explanation for what, at first sight, might appear to be a rather unnecessary task.

After the discovery of the dinosaurs in 1878, and the preliminary announcements concerning this event (P.J. VAN BENEDEN, 1878; E. DUPONT, 1878) the task of the formal description of these dinosaurs was handed to G.A. BOULENGER, vertebrate zoologist at the Musée Royal d'Histoire Naturelle. In 1881, BOULENGER submitted to the Royal Academy of Science a first paper on the anatomy of these dinosaurs, in which he described the anatomy of the pelvis of *Iguanodon* and proposed that the greater number of sacral vertebrae (six) in the Bernissart form, as opposed to the five which R. OWEN had been able to demonstrate in the English species *I. mantelli* VON MEYER, 1832, merited the establishment of a new species *I. bernissartensis*. Unfortunately, this paper was refused publication, although a brief highly critical review summarising G.A. BOULENGER's paper was published by P.J. VAN BENEDEN (1881). Shortly afterwards, BOULENGER accepted a post at the British Museum (Nat. Hist.) and thus the task of description of the Bernissart species passed to Louis DOLLO in 1881. DOLLO published prolifically on the Bernissart fauna: numerous « preliminary notes » were produced on the Bernissart species between 1882 and 1923, ostensibly in preparation for a monographic account of the dinosaurs. However, by 1931, the year of DOLLO's death, no monograph had appeared.

Since the passing of DOLLO, no detailed study of the Bernissart dinosaurs has been attempted. CASIER (1960) produced an interesting review-memoir dedicated to the works of DOLLO. However, although this work included many new and interesting photographs of the Bernissart dinosaurs, it represented merely a synthesis of DOLLO's « notes », rather than a new study and is therefore of little scientific value. QUINET (1972) produced a much condensed booklet based on CASIER's book, but again no new information was forthcoming.

Therefore, up to the present time *Iguanodon bernissartensis* (VAN BENEDEN, 1881) is known only through the « preliminary notes » published by DOLLO. As was pointed out by Hooley as long ago as 1925, DOLLO's papers, although interesting, are not sufficiently detailed to enable comparative work to be done even with species of the same genus, let alone different genera of ornithomimid dinosaur. This present study, therefore, represents an attempt to fill the existing lacuna; this seems to be especially necessary at the present time because several, related, Lower Cretaceous iguanodontoid dinosaurs have recently been discovered in North America (OSTROM, 1970), Asia (ROZHDESTVENSII, 1966), North Africa (TAQUET, 1976) and Australia (BARTHOLOMAI, pers. com). Without anatomical studies of all of these species, questions relating to their phylogeny and palaeogeography will remain purely speculative.

This paper is the first of a series describing the anatomy and relationships of the species of the genus *Iguanodon* and some related dinosaurs.

B — HISTORICAL REVIEW

Discovery and excavation.

The small village of Bernissart lies near the French border, between the larger towns of Mons and Tournai, in the province of Hainaut. Mining has long since ceased at the village, which lies among numerous coal tips that now dominate the landscape. In the spring of 1878, the coal mine at Bernissart was being actively worked and a series of new galleries were being excavated at many of the pits. In particular, a new gallery was being excavated in the « Fosse Sainte Barbe » at a depth of 322 metres, a level which coincided with that of the « Luronne » coal seam. On the 28th February, the regular limestone strata in this gallery passed abruptly into an extremely irregular region, consisting of broken blocks of limestone and coal, intermingled with sands and marls. It was at first assumed that this was a « cran », the local term for small, pocket-shaped geological faults, which abounded in the area. Excavations continued: however, instead of re-entering limestone strata, as expected, the gallery passed into an area of more regularly stratified beds of marl and sands. At this point, the gallery was inspected by the pit manager Gustave FAGÈS and the pit engineer in order to assess the likelihood of this gallery producing coal. Several unusual objects were found during the inspection and were at first thought to be fragments of fossilised wood; many such fragments had already been noticed by the miners:

« A un certain point, un des mineurs, Jules Créteur, rencontra de nombreux ossements imprégnés de pyrite qu'à première vue tous les hommes de l'équipe prirent pour les troncs d'arbres remplis d'or ».

(L.F. DE PAUW, 1902 : 1)

Several specimens were carried to the surface for further examination, and FAGÈS arranged for a small team of miners to return to the gallery to see if any more specimens could be found. Some specimens were sent to F.-L. CORNET, a geologist well-known for his studies of the area; being unable to identify them, he forwarded the specimens to P.J. VAN BENEDEN, a leading comparative anatomist at the University of Louvain (Leuven).

Meanwhile at Bernissart, fossils began to be discovered in large quantities and eventually came to the notice of Gustave ARNOULD, the chief mining engineer of the province, who was preparing a detailed report on the coal-bearing strata of the Mons area (ARNOULD, 1878 pp. 191-194). ARNOULD immediately contacted

Edouard DUPONT, Director of the Musée Royal d'Histoire Naturelle, Brussels.

« Découverte importante ossements dans la faille charbonnage Bernissart se décomposent par pyrite; envoyer Depauw demain pour arriver station Mons huit heures matin.

» Y serai urgent — Gustave ».

(Archives, I.R.Sc.N.B. — Telegram dated : Mons 3.23 p.m., 12 avril, 1878.)

Louis DE PAUW briefly visited Bernissart and returned to the Museum to develop techniques to limit the tendency of these fossils to crumble in air and also to pyritise rapidly.

On the 7th May, VAN BENEDEN (1878) announced the discovery of fossils at Bernissart to a meeting of the Royal Academy of Science. Among the fossils, some teeth could be identified:

« ... quelques dents dont l'émail est conservé nous font croire qu'elles proviennent d'*Iguanodon* ».

P.J. VAN BENEDEN, 1878 : 579.)

Once the importance of this discovery was realised, the board of directors of the mine at Bernissart offered the fossils to the state, and provided both facilities and a team of miners to help with further excavations. On the 15th of May, excavations were recommenced under the direction of DE PAUW, who headed a team of excavators composed of experienced miners and technical staff from the Museum. In August of the same year a strong tremor was felt in the mine, which caused some subsidence, trapping DE PAUW and his team underground for several hours. Shortly after the tremor, flood waters started to seep into the mine until, on October 22nd, all work had to cease because the galleries were completely submerged. The galleries were not re-opened until May 1879, after which excavations continued uninterrupted until 1881; by this time a second gallery at 356 metres had been opened, which produced several more skeletons from a similar, but less extensive fissure.

In 1881 excavations were suspended because there was no longer any room to accommodate the enormous numbers of fossils already recovered. Ventilators and water pumps were maintained in the galleries to await renewed excavations, once new museum buildings had been acquired. A new museum was opened in 1902; however, no further excavations were started before the outbreak of the first World War. During

the German occupation of Belgium, Otto JAEKEL, a German palaeontologist, re-opened excavations at Bernissart in order to collect new fossils for Berlin Museum. Work on a new gallery, between the original ones at 322 and 356 metres was started. However, the fossiliferous marl had not been reached by the time the Allied forces liberated Belgium. During the following decade, attempts were made to renew excavations at Bernissart, but lack of financial support led to the removal of pumping equipment from galleries and the eventual closure of the pit.

Preparation and exhibition.

Several skeletons of *Iguanodon* were found at Bernissart in complete articulation. Each skeleton, as it was uncovered, was assigned a letter, and an outline plan was made as it lay *in situ*. The complete skeleton was then divided into manageable blocks which were encased in plaster and labelled, before being removed and transported to Brussels, where it was re-assembled. The plaster jacket served not only to protect the fossils during transport, but also to prevent the fossils from their tendency to crumble once exposed to air.

In order to prevent pyritic decay, which affected a large proportion of the fossils, each specimen was partly prepared by removing the adhering matrix from one side and then immersed in a heated solution of shellac saturated with arsenic. After an hour the specimen was removed and dried. The matrix was then removed from the remainder of the fossil and the treatment repeated. This treatment appears to have had little effect on the pyritization process, but greatly strengthened the otherwise friable specimens. Areas which were particularly badly pyritised were treated by mechanically chipping away the pyrites and filling the treated areas with « carton pierre », a mixture of shellac and talc.

During the period 1884-1890, a continuous record of the condition of various specimens which were put on display at the Museum reveals that pyritic decay was a continuing problem. By the early 1930's the state of preservation of these dinosaurs was causing concern, for many of the skeletons were showing signs of progressive deterioration. These were treated by further application of shellac. The collections were also enclosed in enormous glass cases, so that variations in humidity and temperature, which were thought to accelerate the decomposition, were reduced to a minimum. During the last half century the Bernissart fossils appear to have decayed relatively little. The majority of the specimens are, however, in such a fragile state that they are almost impossible to study. It is clear that a long-term, very careful programme of conservation needs to be undertaken so that the collections can be of use scientifically, and also to prevent

a gradual process of decay which appears, at the present time, to be destroying the skulls of many of the better preserved specimens.

Literature review.

After the publication of preliminary reports on the discovery of fossils at Bernissart (VAN BENEDEN, 1878; ARNOULD, 1878, and DUPONT, 1878) there was a short lapse before a review of an anatomical study on *Iguanodon*, which had been started by BOULENGER, was published by VAN BENEDEN (1881). In the review it was revealed that BOULENGER wished to propose that a new species, *Iguanodon bernissartensis*, be created to account for the anatomical differences between the specimens discovered at Bernissart, and those attributed to *I. mantelli* which had been found in England (see OWEN, 1841, 1855). In the following year DOLLO commenced the description of the new Belgian specimens with the first of a long series of preliminary notes; these appear to have centred around a series of five short papers. The first (DOLLO, 1882) showed (i) the differences between the two species *I. mantelli* and *I. bernissartensis*, both of which were represented in the Bernissart collection; (ii) the similarities between the Belgian *I. mantelli* (IRSNB. 1551) and that from England (BMNH. R. 3741) and, (iii) that *I. bernissartensis* (VAN BENEDEN, 1881) and *I. seelyi* (HULKE, 1882), were synonymous and that *I. bernissartensis* therefore had priority. The second note (DOLLO, 1882a) was solely concerned with the pectoral girdle and its construction, more particularly the sternal plates, which MARSH (1881) had interpreted as clavicles. In the third note (DOLLO, 1883a) an analysis of the pelvis and hind limb was made in order to deduce the correct posture and gait of *Iguanodon*; this had been stimulated by the controversy over dinosaurian posture and gait between COPE (1866, 1869), HUXLEY (1868, 1870) and OWEN (1877). In view of the structure of the manus, the nature of the vertebral column and the bipedal dinosaur trackways from the Wealden of England (BECKLES, 1862), DOLLO concluded that *Iguanodon* was a biped. The fourth note (DOLLO, 1883b) consisted of a brief attempt to describe the skull of *I. bernissartensis* and an even more brief description of the vertebral column. Finally, the fifth note (DOLLO, 1884) consisted of a description of the proatlas and a discussion of the jaw musculature of *Iguanodon* in relation to the structure of the cranium and diet.

In addition to these notes, DOLLO published a large number of short papers on the anatomy and physiology of *Iguanodon*. These comprised papers on the pectoral girdle (DOLLO, 1885, 1886, 1886a), on ossified tendons (DOLLO, 1887 a, 1887b, 1890), on the stance, gait and functional anatomy of the hind limb (DOLLO, 1883, 1887, 1888, 1906 and 1908), plus several more general papers: DOLLO, 1883c, 1884a, 1884b, 1885a, 1885b,

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1888a, 1909 and 1919. Finally, DOLLO (1923) commemorated the centenary of the original discovery of *Iguanodon* with a short, annotated paper reviewing the anatomy of *Iguanodon*.

Apart from the « popular » booklets, published by CASIER (1960) and QUINET (1972), no detailed anatom-

ical studies of Bernissart dinosaurs have been made since the time of DOLLO, even though lengthy works have appeared on various elements of the flora and fauna e.g. LAMEERE and SEVERIN (1897) on the insects, SEWARD (1901) on the plants, BERTRAND (1903) on coprolites and TRAQUAIR (1911) on the fish.



C — OSTEOLOGY

Order ORNITHISCHIA
Suborder ORNITHOPODA
Family IGUANODONTIDAE
Genus IGUANODON

A full systematic review of the genus *Iguanodon* and the family Iguanodontidae has been prepared elsewhere (NORMAN, in prep.) and is not included within this present account.

Species IGUANODON BERNISSARTENSIS

- 1881 *Iguanodon bernissartensis* VAN BENEDEN : 606.
1882 *Iguanodon bernissartensis* DOLLO : 172.
1969 *Iguanodon bernissartensis* STEEL : 17.

Horizon. — Bernissartian of Belgium; Hauterivian - Lower Aptian of Southern England. Also known from the Lower Cretaceous of Central Asia (ROZHDESTVENSKII, 1952); Spain (LAPPARENT, 1960); fragmentary findings indicate that the species may also occur in France (LAPPARENT and STCHEPINSKY, 1968); Portugal (LAPPARENT and ZBYSKEWSKI, 1957); North Africa (LAPPARENT, 1960) and North America (GALTON and JENSEN, 1975), and finally, on the dubious evidence of footprints alone, from Spitzbergen (LAPPARENT, 1962) and South America (CASAMIQUELA and FASOLA, 1968).

Emended Diagnosis. — Maximum length 11 metres. Double supraorbitals (palpebrals). Number of vertical tooth rows in maxilla and dentary variable, with a maximum of 29 in the maxilla and 25 in the dentary. Sacrum composed of eight fused vertebrae. Scapula, unexpanded distally, proximal region of shaft considerably thickened. Intersternal ossification present. Forelimb, long (approx. 70% of length of hindlimb) and stoutly constructed. Carpals co-ossified. First metacarpal fused to carpals. Phalangeal count of manus : 2, 3, 3, 2, 4; first phalanx of digit I consists of a thin, warped plate of bone, which lies in a shallow recess in the proximal surface of the unguis phalanx. The latter has the form of a long, curved, conical spine which can freely articulate against the fused carpo-metacarpus. Unguis phalanges of digits II and III are broad, rather hoof-like and twisted longitudinally. Hind end of ilium pointed in lateral aspect, with a broad brevis shelf. Anterior ramus of the pubis relatively narrow, proximally transversely flattened, but

with a moderately expanded distal end. Three distal tarsals present. Metatarsal I reduced and transversely flattened, metatarsal V absent.

SPECIMENS USED FOR DESCRIPTION.

The skull description which follows is the result of a thorough study of all the cranial material collected from Bernissart and now housed in the Institut Royal des Sciences Naturelles, Brussels. Although these specimens appear, superficially, to be quite well preserved, many cannot be studied adequately because the interior of the skulls has never been cleared of matrix. The result has been that most of the skulls are decayed to the point where they are now almost too fragile to handle. Fortunately, it has proved possible to supplement the information gained from studying all the Belgian specimens with that from a few specimens collected in Southern England and now in the collections of the British Museum (Nat. Hist.). Even with the British specimens of this species, it has proved impossible to describe completely the osteology of the skull especially the neurocranium. It has been necessary, therefore, to supplement the description with information from the skull of the closely related species. *I. mantelli* (VON MEYER, 1832); when this has been done, an indication has been made in both the text and the figures. A full description of *I. mantelli* is to follow shortly.

The postcranial skeleton of many specimens of *I. bernissartensis*, although not perfect, is far better preserved than the skulls, and reference to a variety of specimens, notably the Holotype (IRSNB. 1534), IRSNB. 1561, IRSNB. 1536 and « Individual S » (from the conservatoire collections) has permitted an almost complete osteological description.

THE SKULL AND LOWER JAW.

General description.

The skull of *I. bernissartensis* is approximately 85 cms long in adult specimens and bears a superficial resemblance to that of a large horse (fig. 2). Its shape is that of a tapering oblong, which narrows toward the tip of the snout. Passing backward from the snout, the upper border of the skull extends upward and backward in a gradual curve to a point above the orbit, and then extends almost horizontally backward as a

flat table formed by the roof of the braincase and the upper temporal arches. The posterior border of the skull is quite deep and, as a result, the jaw articulation is displaced considerably below the occlusal plane of the tooth rows. Each quadrate (fig. 2, Q) forms a postero-lateral corner to the skull, descending almost

orbits. A narrow gap persists between the orbital margin and the adjacent medial edge of the first supra-orbitals (fig. 3, So. 1); this appears to have been filled by connective tissue.

In lateral view (fig. 2) the skull displays three prominent and two lesser apertures. The external naris

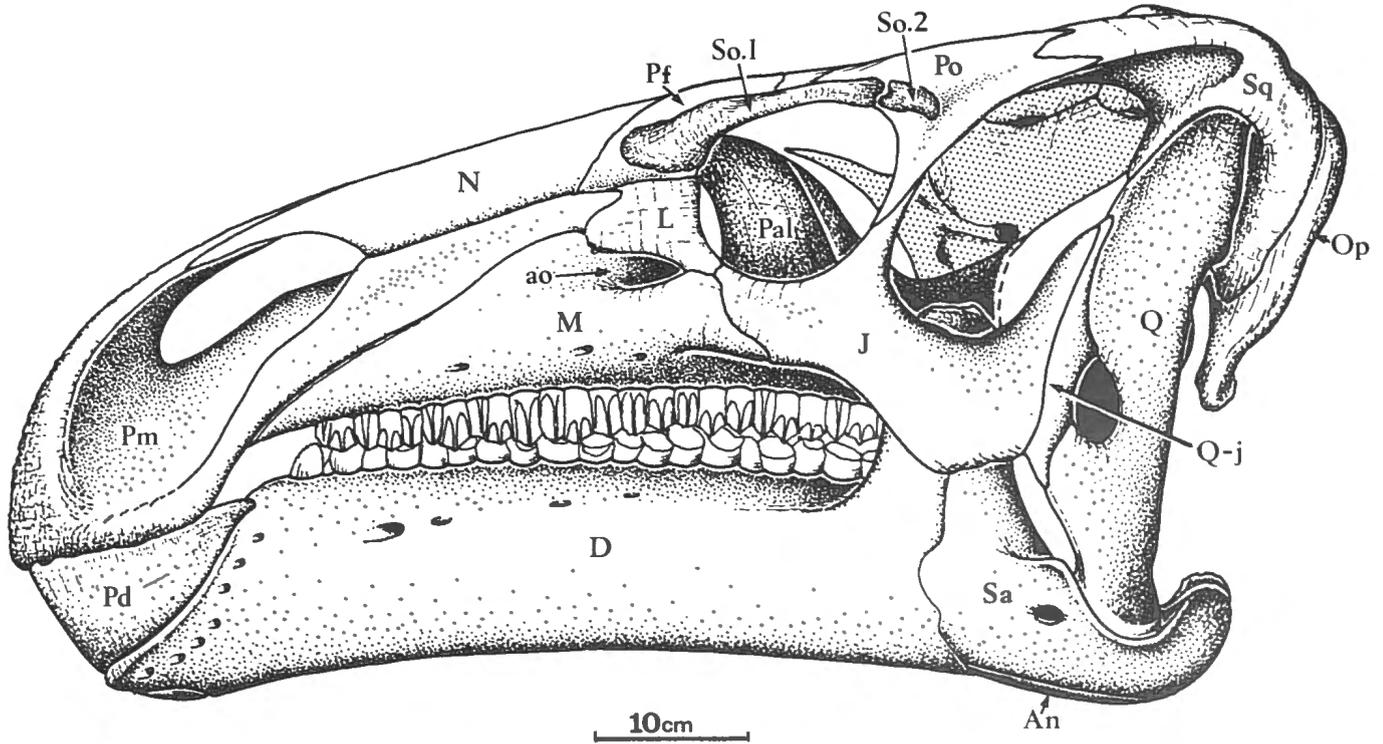


FIG. 2. — *Iguanodon bernissartensis*. Skull reconstruction, based mainly on : IRSNB. 1561, 1536, 1535. For abbreviations see alphabetical index, section G.

vertically from a socket in the squamosal (fig. 2, Sq). The upper end of the quadrate is overhung posteriorly by a massive, hooked and wing-like paroccipital process. Between paroccipital process and quadrate there is a deep V-shaped notch, which probably supported the tympanic membrane. With the lower jaw removed, the lower border of the skull forms a shallow arch; anteriorly, this is modified by a step, where the premaxilla projects below the scalloped, tooth-bearing margin of the maxilla; posteriorly, there is also a discontinuity between maxilla and quadrate, which is spanned by the jugal arch.

In dorsal view (fig. 3) the skull can best be described as consisting of two roughly oblong portions. Posteriorly, there is a broad rectangular section formed by the elements surrounding the braincase and orbits; this is perforated on either side of the fused parietals by the supratemporal fenestrae, a pair of ellipsoid slits. Anteriorly, there is a narrower rectangular area roofing the nasal and buccal cavities; this ends in the rounded premaxillary beak, which flares out beneath the narial openings. The supraorbital bones (fig. 3, So. 1, So. 2) form a supero-lateral roof to the orbital cavities and add considerably to the width of the skull above the

is very large, ellipsoid in outline, trumpet-shaped and faces antero-laterally. A thick bony septum separates the narial channels anteriorly. Behind the narial openings and below the lachrymal (fig. 2, L) there is a small antorbital aperture, which forms the outlet for a channel directed obliquely forward and downward from (or to) the orbit onto the surface of the maxilla. The orbit is large and rounded (contrary to the opinion of DOLLO, 1883*b*) and is situated high on the side of the skull. The first supraorbital (fig. 2, So. 1) follows the contour of the antero-dorsal margin of the orbital cavity and tapers to a truncated rugose end, lateral to the surface of the postorbital; a small accessory supra-orbital (fig. 2, So. 2) lies immediately behind the first and seems to have been held in place against the postorbital by connective tissue. Behind the orbit there is a lateral temporal fenestra, which is large, oval and somewhat obliquely inclined. Elements of both the palate and braincase are visible through the orbit and lateral temporal fenestra. A small, elliptic, quadrate foramen is found between the quadrato-jugal and quadrate.

In posterior view (fig. 4 B) the occiput is quite a large, broad plate, flanked on either side by the greatly

expanded opisthotics (Op) which form most of the paroccipital processes. Thin, wing-like exoccipitals form a transverse bar above the foramen magnum and lie against the opisthotics. The supraoccipital (fig. 4 B, Su) is cryptically positioned at the back of the braincase above and anterior to the exoccipitals. A post-temporal opening (fig. 4 B, vcd) cannot be positively identified in any of the specimens from Bernissart; however, there is some evidence from British material which suggests that there was a small pair of openings in the occiput, on either side of the supraoccipital, which may correspond to the remnant of the post-temporal fenestra in sauropsids. The foramen magnum is a large dorsoventrally elongate ellipse beneath which is the large, globular occipital condyle. The quadrates are pillar-like and hang down on either side of the occiput from the paroccipital wings.

of each battery (pls. 2-4). The mandible becomes broader posteriorly, producing a large, rounded shelf below and lateral to the teeth; this forms the lower part of the cheek recess, referred to above. Toward the hind end of the jaw, a large coronoid process projects upwards into the lateral temporal fenestra (fig. 2). Behind, the coronoid process descends steeply to the shallow, bowl-shaped depression for the jaw articulation (pl. 4). Immediately behind this glenoid there is a small upturned retro-articular process. The mandibular (adductor) fossa, beneath the coronoid process, is large and open. (pl. 4, ad. f).

The detailed osteology of the skull has been divided into five sections, in order to present a more manageable format. The sections are: the *Neurocranium*, comprising the supraoccipital, exoccipital, opisthotic, proötic, parietal, frontal, basioccipital, basisphenoid,

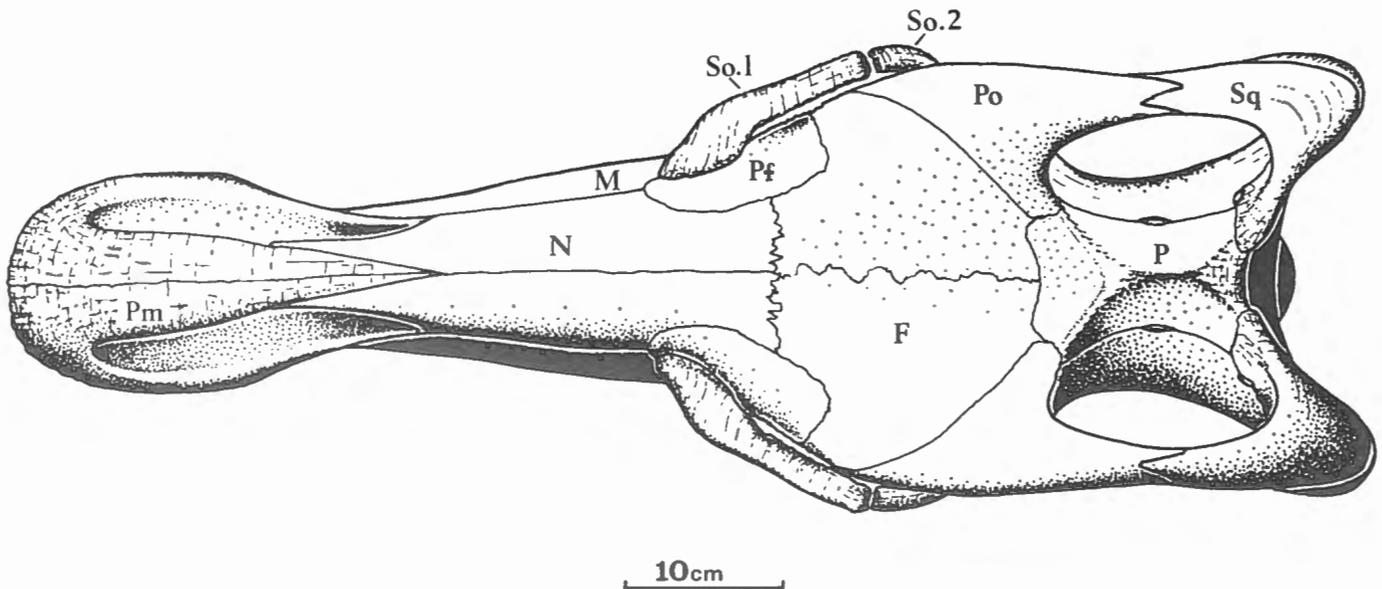


FIG. 3. — *Iguanodon bernissartensis*. Skull reconstruction in dorsal view.

Ventrally (fig. 5) the edentulous premaxillary « beak » is moderately vaulted and passes backward into a long, narrow naso-buccal cavity which is highly vaulted. The upper, nasal, cavity is divided by a thin median keel of bone formed of the vomers (fig. 5, V). On either side of the upper jaw, the lateral surfaces of the maxillae bulge outward noticeably, producing cheek recesses lateral to the teeth; these are found in many ornithischian dinosaurs (GALTON, 1973).

The lower jaw is a stout structure (figs. 2, 9; pls. 1-4). The toothless anterior portion is capped by a sharp-edged, crescent-shaped prementary (Pd) which binds both jaws together — in addition to the dentary symphysis. The teeth are borne in long ranks along the inner edge of each jaw and are arranged in a partially interlocking battery of functional and replacement teeth. The occlusal edges of the tooth rows of each jaw are straight and run parallel for the greater part of their length, but curve outwards at the hind end

orbitosphenoid, parasphenoid and laterosphenoid; the *Maxillary segment* comprises the remaining skull bones which are not directly involved in the formation of the braincase; the three remaining sections (*Mandible*, *Accessory elements* and *Dentition*) are self-explanatory.

The Neurocranium.

In the reptilian skull the *supraoccipital* has its origin in the cartilage of the synotic tectum lying above the foramen magnum and between the otic capsules, from which it is ultimately derived. When fully developed, it extends forward beneath the skull roof and laterally to meet the otic bones and enclose the upper portions of the semi-circular canals of the inner ear.

In *I. bernissartensis*, the supraoccipital is located in a deep recess in the hind end of the braincase, between the parietals, opisthotics, squamosals and

exoccipitals (fig. 4 B, Su). It is excluded from the dorsal margin of the foramen magnum by a horizontal bar formed by the fused exoccipitals. The poor preservation of this region of the skull in all specimens of this species makes it impossible to define precisely its sutural relations with the surrounding bones of the occiput. In occipital view (fig. 4 B) the supraoccipital is restored as a broad symmetrical bone, inclined forward and upward beneath the parietal. As can be seen in fig. 6, A and B, its ventral surface is slightly convex and rests upon the exoccipital bar. Along the midline of its postero-dorsal surface there is a broad, rounded mound with a narrow median ridge, which appears to abut against the postero-ventral margin of the parietals; this whole structure may be homologous with the ascending process of the synotic tectum. On either side of this « ascending process » the surface of the supraoccipital sweeps downward and outward, leaving channels on either side, before curving upward to meet the opisthotics laterally and the squamosals above.

cimen also shows its sutural relationships to the surrounding occipital bones; similar relationships are suspected for *Iguanodon*.

The *exoccipitals* (E - figs. 4 B, 8; pls. 3, 4) meet dorsally and ventrally, forming the entire margin of the foramen magnum. Above the foramen magnum, they appear to form a transverse bar which projects laterally to form thin, winglike plates behind the opisthotics, similar to that seen in the primitive hadrosaur *Bactrosaurus* (GILMORE, 1933; fig. 23). The ventral border of each of these wings curves inward and downward to the pillar-like lateral walls of the foramen magnum. Ventrally, the internal edges of these pillars produce thin sheets of bone flooring the endocranial cavity. The suture between exoccipital and opisthotic along the lateral wall of the braincase is not preserved but probably existed along the *Vagus* (Cranial nerve X) foramen, which normally marks the position of the fissure separating otic and occipital cartilages (see fig. 9). There is evidence to suggest that

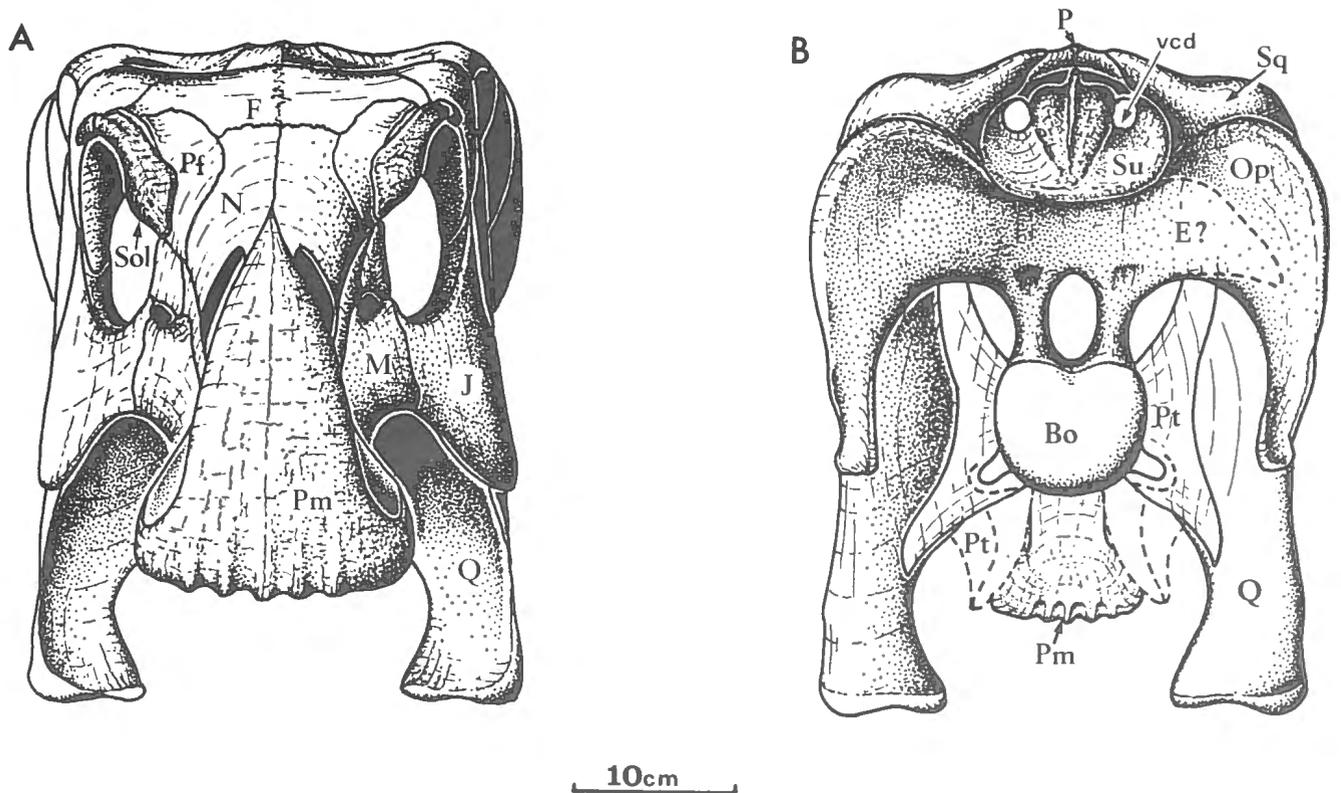


FIG. 4. — *Iguanodon bernissartensis*. Skull reconstruction. A : anterior view; B : posterior (occipital) view. Broken lines indicate imperfectly known regions.

The construction of the occiput in *Iguanodon* is most similar to that seen in hadrosaurs, and comparison of the supraoccipital in these forms with that of *Iguanodon* has proved helpful. LANGSTON (1960) described an isolated hadrosaur supraoccipital (fig. 7 a, b); its salient external features correspond to those already noted in *Iguanodon*. However, this fine spe-

at least two branches of the *Hypoglossal* (cranial nerve XII) exit through the exoccipital (NORMAN, in prep.).

The *parietals* (P - figs. 3, 8, 9; pl. 4) form a single, fused oblong plate with a raised median ridge (sagittal crest) which caps the braincase; its lateral walls slope away ventro-laterally and form the dorsal part of the inner wall to the supra-temporal fenestra. The lateral

BERNISSARTENSIS FROM THE LOWER CRETACEOUS OF BERNISSART (BELGIUM)

walls are sutured to the elements of the lateral wall of the braincase along a well-defined cleft. Anteriorly and posteriorly, the parietal plate produces short, stout wings, which meet the postorbitals and squamosals respectively, while in the midline they meet the frontals anteriorly and the supraoccipital postero-ventrally.

ovalis, into which fits the footplate of the stapes. Posteriorly, and dorsal to this foramen, there develops a prominent projection, the *paroccipital process*; its major part is formed by the opisthotic. Behind the paroccipital process, the opisthotic meets the exoccipital medially and the supraoccipital dorsally.

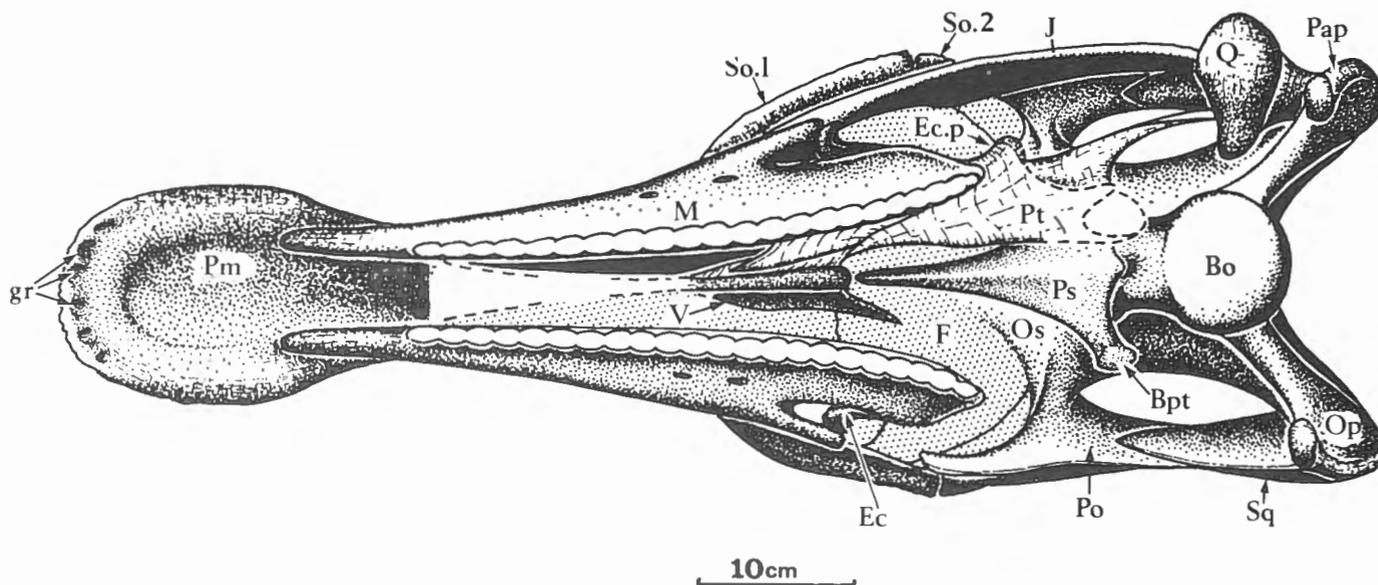


FIG. 5. — *Iguanodon bernissartensis*. Skull reconstruction, in ventral view, lower jaws removed. Broken lines indicate imperfectly known regions.

The *frontals* (F - figs. 3, 4 A; pl. 4) are firmly sutured together along the midline and form a very broad, flat plate. The nasals overlap the frontals in a broad, transverse suture (fig. 9). Lateral to the nasal suture, the frontals meet the prefrontals in a short, transverse suture which extends to the orbital margin (fig. 3). After forming a very short section of the orbital margin, the frontals meet the postorbitals. The suture between these bones is long and curves medially, skirting the edge of the supra-temporal fenestra; converging from both sides, the frontals have a short transverse suture with the parietal plate in the midline.

The ventral surface of the frontals is moulded into a series of ridges and depressions which roof the olfactory and orbital cavities. This area is preserved as a natural mould in one very fine specimen, BMNH. R. 8306. Posteriorly, in the midline, there is a short longitudinal channel, which forms an extension from the endocranial cavity housing the paired olfactory nerves; farther forward, this channel expands into two broad concave depressions which house the olfactory bulbs; these latter are separated by a low, median, keel of bone. Lateral to the olfactory areas there are broad, shallow concave areas which form the roof of the orbits.

Typically, the *proötic* and *opisthotic* together form the *otic capsule*: the thickened side wall of the braincase, which houses the major portion of the inner-ear structures. Between these two bones lies the *fenestra*

In *I. bernissartensis*, none of the skulls is sufficiently well preserved to allow precise description of the bones of the otic capsule (see pls. 1, 3). The reconstructed skull (fig. 9) shows the lateral wall of the braincase restored by reference to *I. mantelli*, for which adequate material is known. The proötic part of the otic capsule meets the laterosphenoid anteriorly, the parietal dorsally, and the basisphenoid and basioccipital ventrally. The opisthotic portion meets the parietal, squamosal and supraoccipital dorsally, the exoccipital posteriorly and the basioccipital ventrally.

A description of the precise composition of the paroccipital process in ornithopods has proven difficult to resolve in several instances (GILMORE, 1909; LANGSTON, 1960; OSTROM, 1961; TAQUET, 1976). In the contemporary, yet generalised ornithopod *Hypsilophodon* (GALTON, 1974) the paroccipital process appears to be formed of the opisthotics alone and is therefore « paroccipital » in its original sense. However, in *Camptosaurus* (GILMORE, 1909), a form which appears to be intermediate in terms of its anatomy between *Hypsilophodon* and *Iguanodon*, the exoccipital and opisthotic are completely fused and apparently contribute equally to the paroccipital process. In hadrosaurs (LANGSTON, 1960) which are structurally more advanced than *Iguanodon*, the exoccipital appears to form the major part of the process. In *Iguanodon*, the evidence is equivocal. In several skull specimens (IRSNB. 1535, 1561, 1562) the exoccipital and opistho-

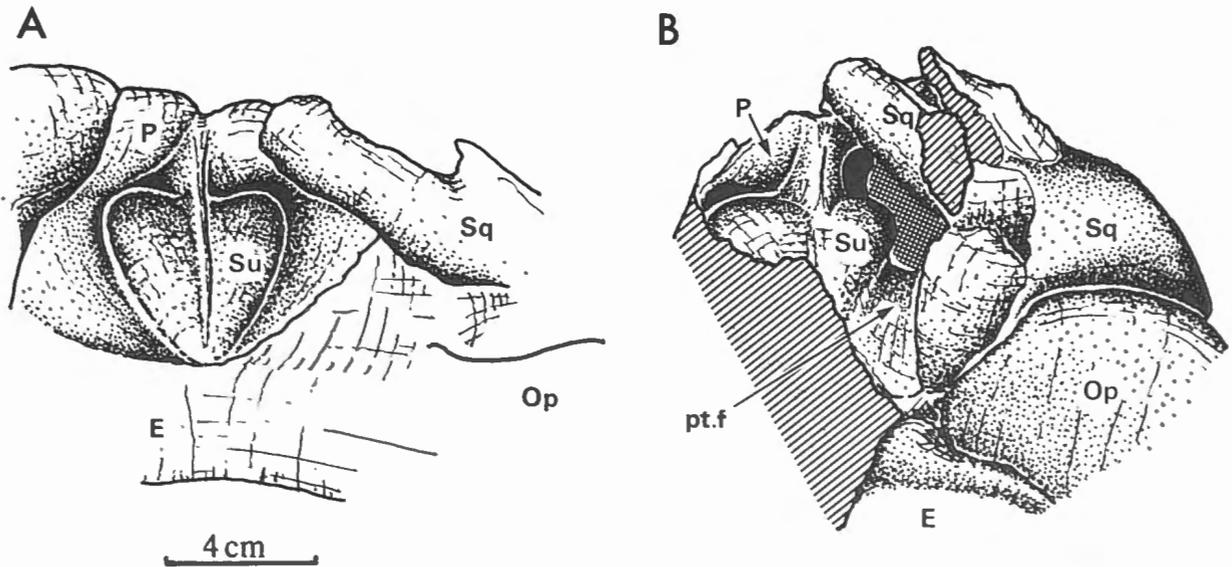


FIG. 6. — *Iguanodon bernissartensis*. The occipital region of A, IRSNB. 1535 (en gisement); B, IRSNB. 1561 (monté).

tic bones seem indistinguishably fused. However, in IRSNB. 1536 (pl. 4; fig. 8) the exoccipital seems identifiable as an horizontal bar, backing on to the opisthotic behind the paroccipital wing, implying that the opisthotic forms the entire paroccipital process. The only explanations possible appear to be either that the apparent arrangement of the occipital bones in IRSNB. 1536 is misleading and can be attributed to *post-mortem* crushing and fracturing or that the development of the paroccipital process in *Iguanodon* is subject to some variation. With regard to the second possibility, OSTROM (1970) drew attention to some variability in the construction of the occiput of *Tenontosaurus*; however, it should also be noted that this was OSTROM's opinion after a cursory study of specimens which seem to have suffered mozaic fracturing, thereby making identification of suture lines rather difficult.

The *laterosphenoid* (La - pl. 1; fig. 9) forms the anterior half of the lateral wall of the braincase and, as in all archosaurs, this bone forms as an ossification of a pre-otic cartilaginous band, the *pila antotica*. Although this region of the braincase is not well preserved in *I. bernissartensis*, the laterosphenoid undoubtedly had sutural relationships similar to those seen in *I. mantelli*: it is sutured to the parietal dorsally, the orbitosphenoid anteriorly, the basisphenoid ventrally and the proötic posteriorly. The general area of the braincase wall occupied by the laterosphenoid curves forward and outward, forming the inner, and part of the anterior, wall to the temporal cavity. Along the ventral edge, where it meets the basisphenoid, there is an horizontal trough, which extends forward from the large Trigeminal foramen found at the ventral edge of the junction of laterosphenoid with proötic; this

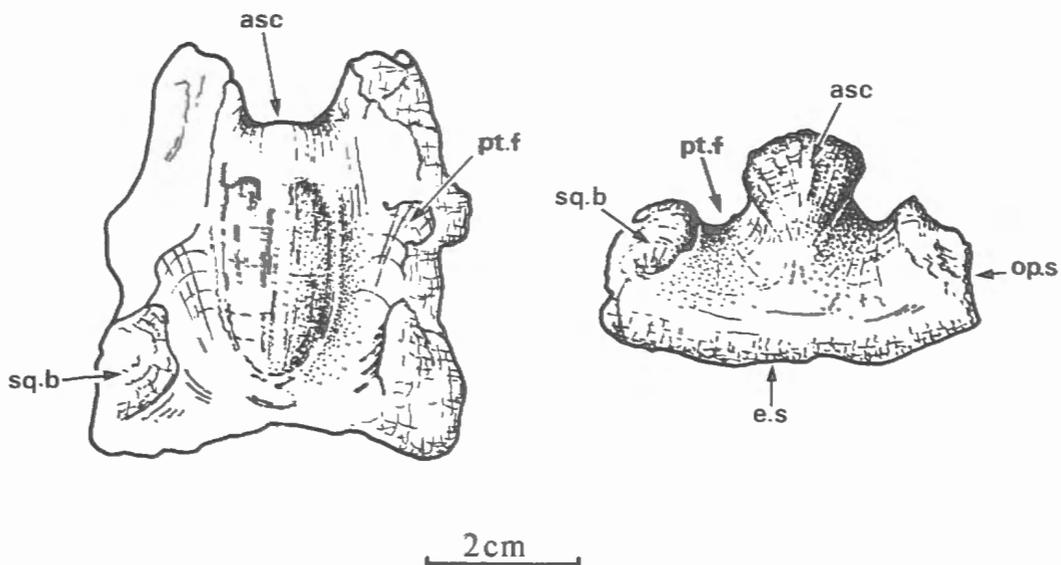


FIG. 7. — The supraoccipital of an unidentified hadrosaur. Redrawn from LANGSTON (1960). Plate 34, figs. B, E.

trough carried the ophthalmic branch (V_1) of the Trigeminal nerve (pl. 1, V_1).

At the junction between parietal, laterosphenoid and proötic, there is an elliptical foramen (fig. 9, paf) indications of which can be seen in IRSNB. 1561 (pl. 1, paf) this passes through the cranial wall into the dorso-lateral region of the endocranial cavity and marks the point of entry of the *vena capitis dorsalis*.

The *orbitosphenoid* (Os - figs. 5, 9) develops in or above the *pila metoptica*, a cartilaginous band in the embryo reptile, which arises between the optic and metoptic (oculomotor) fenestrae. The area of the braincase of *I. bernissartensis* occupied by the orbitosphenoid is quite well shown in IRSNB. 1536 (fig. 10). Situated on the antero-ventral floor of the braincase, this bone forms a curved plate at the back of the orbital cavity. It is sutured to the frontal and laterosphenoid above and laterally, to the basisphenoid posteriorly and to the parasphenoid ventrally. Several cranial nerves pierce this plate in *I. mantelli*, but in *I. bernissartensis* only the foramen for the Trochlear (Cranial nerve IV) can clearly be discerned (fig. 10, IV).

OSTROM (1961) identified the septosphenoid (presphenoid) as an ossified plate anterior to the orbitosphenoid, in the sphenethmoid region of the skull of the hadrosaur *Corythosaurus*. However, no such ossification appears to have been present in any of the skulls of *Iguanodon*.

Typically, the *parasphenoid* forms a sheet of dermal bone on the undersurface of the braincase and is frequently fused indistinguishably with the basisphenoid. The parasphenoid of *Iguanodon* can be seen in some detail in *I. bernissartensis* (Ps - pls. 1, 2; figs. 5, 9 and 14) so that its general shape can be defined, even though its sutural contacts cannot. In ventral view, it has the form of an isosceles triangular plate, with its base facing posteriorly. Its postero-lateral corners are produced into tapering processes, which support, and in *I. mantelli* appear to sheath, the *basipterygoid processes* (Bpt) which are normally formed of the basisphenoid alone. Anteriorly, the parasphenoid tapers to a narrow elongate rostrum (cultriform process) which extends between the orbits and probably supported a cartilaginous septosphenoid.

The *basisphenoid* (Bs - fig. 9) forms the central portion of the floor of the braincase and is sutured against the basioccipital posteriorly, the proötic and opisthotic dorsally, the orbitosphenoid anteriorly and the parasphenoid ventrally. Unfortunately, few of the characteristic features of the basisphenoid are well preserved in any of the Belgian specimens (pl. 2). Ventrally, in the region of the suture to the basioccipital there are a pair of large swellings (*basal tubera*) for attachment of subvertebral muscles. In some instances it is possible to see the aperture for the Vidian canal, which carries the internal carotid artery and palatine branch of the Facialis (Cranial nerve VII) through the basisphenoid into the pituitary fossa.

Above this foramen there is a broad crescent-shaped muscle scar which curves downward and forward from the Trigeminal foramen, and serves as an area of origin for a portion of the Constrictor Dorsalis musculature.

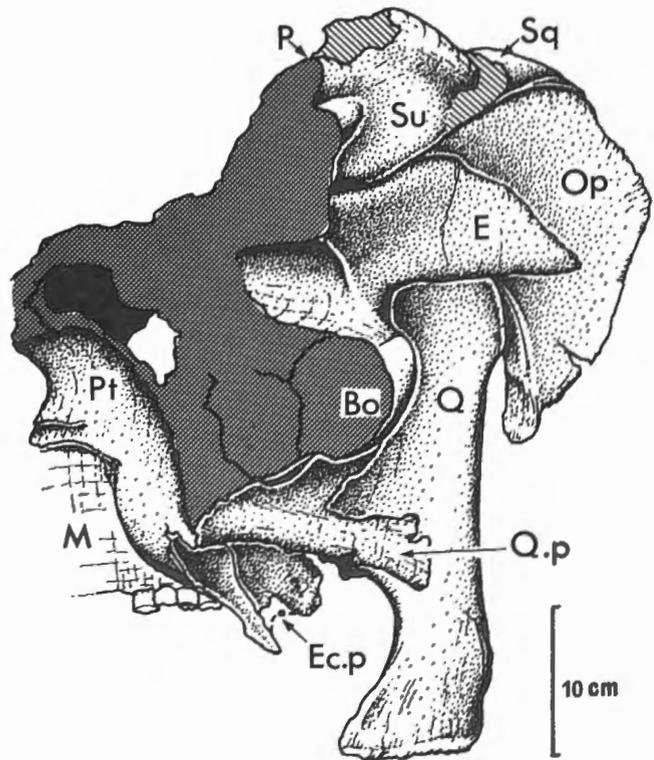


FIG. 8. — *Iguanodon bernissartensis*. IRSNB. 1536. Postero-medial view of the occipital region of the skull. Cross-hatching indicates broken bone surface; even stippling indicates longitudinal section.

The *basioccipital* (Bo - pls. 2-4; figs. 4 B, 5, 9) forms the posterior part of the basicranial axis and most of the occipital condyle. It is sutured to the exoccipitals and opisthotics dorsally, and the basisphenoid anteriorly. The occipital condyle is large and rounded, with dorsally a broad notch forming the floor to the neural canal. The bases of the exoccipitals extend onto the dorsal margin of the occipital condyle and meet in the midline, excluding the basioccipital from the foramen magnum. Forward of the condylar region, the sides of the basioccipital contract before meeting the basal tubera.

The Maxillary Segment.

The *premaxillae* (Pm - pls. 1-4; figs. 2-5, 9) are complex rather elongate bones in *Iguanodon*, as they are in most ornithischians. They are sutured together medially, and anteriorly consist of a broad, domed, edentulous beak region which is deeply excavated on either side by the external nares. Three paired processes are produced posteriorly, one pair superior, the other two inferior.

The buccal margin of the premaxillae has a broad spoon-shaped appearance in occlusal view (fig. 5). The

U-shaped occlusal arcade is thickened posteriorly, but becomes narrower and more trenchant rostrally, where an irregular but quite sharp cutting edge is formed. Immediately behind the sharp anterior edge there are a series of scoop shaped depressions (fig. 5, gr) which decrease in size laterally. Behind the beak margin, the premaxillae are quite deeply vaulted and form a hard palate roofing the anterior buccal cavity. The surface of the premaxillae external to the beak margin is roughened and puckered (figs. 2, 3), indicating an area for attachment and growth of a horny beak which sheathed these occlusal margins.

Dorsally (fig. 3) between the external nares, there is a tapering process formed from both premaxillae. Anteriorly, this is supported by an internasal septum, but farther posteriorly it is produced into a long, narrow, wedge between the nasal bones, becoming completely overlain by the nasals posteriorly. Long, thin, flat facets for attachment of the nasals are found on the ventro-lateral surfaces of this process (IRSNB. 1731 - CASIER, 1960 : pl. XII, no. 4).

Beneath the external nares, the lateral surface of each premaxilla produces an elongate process, which forms a long oblique contact with the maxilla, terminating at the lachrymal posteriorly and contacting the nasal dorsally. Medial to these processes there is another posterior process in the ventral midline, formed of both premaxillae, which prolonged the hard palate above the anterior portions of the maxilla; this median process probably contacted the vomers (see figs. 5, 9).

The *maxilla* (M - pls. 1-4; figs. 2-5, 9) is the stoutest of the skull bones. It is a long, wedge-shaped bone, along the slightly arched ventral edge of which are the tooth sockets. In ventral view, the teeth form a very slightly curved blade which becomes noticeably hooked outward at the hind end (pl. 3; fig. 5). The medial surface of the maxilla is vertical and smooth; above the alveolar margin there is an arcade of small foramina (fig. 9, for) the position of each of which corresponds to that of a vertical tooth row. These have been interpreted by Edmund (1957) as foramina for the entry of nutritive blood vessels and sensory nerves to the dental lamina. All the foramina are linked together by a groove which presumably marks the path taken by the main blood vessel and nerve trunk supplying these foramina. The area between these nutritive foramina and the alveolar margin forms a thin alveolar parapet (Ap) which supports the successional and functional teeth. The surface of this parapet is covered by low, fine ornamentation, totally unlike that of the rest of the maxilla and only found on a similar parapet on the medial surface of the lower jaw. Most probably, the irregular texture of this bone is related to the metabolic demands made on the alveolar tissue. The continuous tooth replacement pattern implies a rapid turnover of minerals for the processes of deposition and resorption of minerals within the alveoli, and concomitant changes in the alveolar bone which was constantly being remodelled to support the continuously growing teeth.

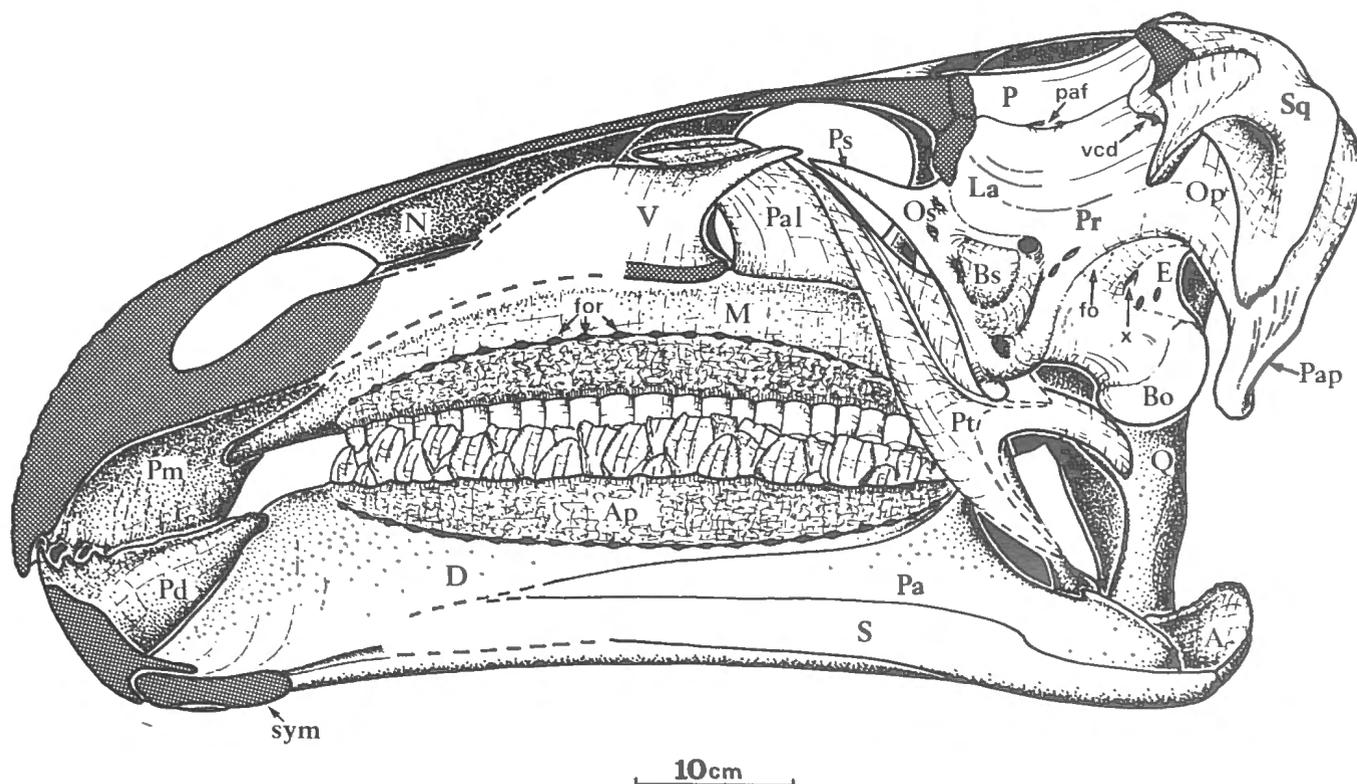


FIG. 9. — *Iguanodon bernissartensis*. Reconstruction of the skull which has been partly dissected to reveal the content of the naso/buccal cavities and the structure of the braincase. Detailed structure of braincase from *I. mantelli* (BMNH. R. 2501). Even stippling represents « cut » bone surface.

Anterior to the alveolar region, the maxilla tapers to a blunt point which lies beneath the premaxilla. The upper surface of this process rises upward as it passes backward, forming a long straight suture with the premaxilla and ending where it meets the lachrymal. The lachrymal spans a shallow trough (antorbital foramen) which passes from the external to the internal surface of the maxilla, just anterior to the orbit.

Posterior to the lachrymal, the maxilla produces a stout lateral process, which supports and articulates against the jugal (fig. 5). Medially, the main body of the maxilla is sutured to the palatine and pterygoid along its dorsal edge (pl. 2; fig. 9); this edge descends to meet the alveolar border at its extreme posterior end. Laterally, the hind end of the maxilla slopes downward and outward and appears to have been sutured with the ectopterygoid (from *I. mantelli*).

The broad triangular lateral surface of the maxilla bulges outward in its dorsal half; below this area, in the region above the alveolar margin, the surface is recessed so that the body of the maxilla considerably overhangs the tooth rows (figs. 2, 5). Several of the more conspicuous foramina on the maxilla open out along the dorsal edge of this maxillary «cheek» recess.

The *nasals* (N - pls. 1, 3, 4; figs. 2, 3, 9) are long, narrow, arched bones, fused together along the midline for most of their length and forming a considerable portion of the roofing to the snout. Each nasal extends from the middle of the dorsal margin of the external naris posteriorly to the frontal suture above the middle of the orbit (fig. 3). Anteriorly, the nasal tapers to a point which lies against the superior process of the premaxilla. Its anterior border curves back and downward, forming the posterior margin of the external naris and meeting the posterolateral premaxillary process. The contact between nasal and premaxilla appears not to have been firmly sutured and is therefore more liable to *post-mortem* displacement (IRSNB. 1536, 1561 — this feature is also found in *I. mantelli*). Posteriorly, the naso-premaxillary suture ends at the point where nasal meets prefrontal. The suture with the prefrontal curves upward and inward across the skull to meet the frontals in a broad, overlapping, transverse suture (BMNH. R. 8306).

The *lachrymal* (L - pls. 1, 4; fig. 2) appears to be a rectangular bone forming the antero-ventral margin of the orbit. A large lachrymal duct can be seen in several specimens but little else of its structure can be discerned from the specimens available. The lachrymal rests upon the maxilla and forms the dorsal border of the antorbital foramen; it contacts the jugal (from *I. mantelli*) posteriorly and the prefrontal dorsally; and anteriorly it is overlain by the premaxilla. The prefrontal-lachrymal suture appears to be rather weak (as with naso-premaxillary suture) and is similarly prone to *postmortem* dislocation.

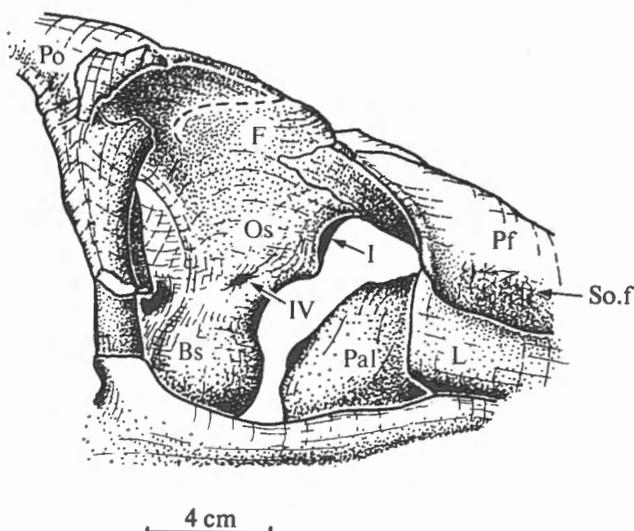


FIG. 10. — *Iguanodon bernissartensis*. (IRSNB. 1536).
Orbital region of the skull. Broken line indicates approximate area of suture between Frontal and Postorbital.

The *prefrontal* (Pf - pls. 1, 3, 4; figs. 2, 3, 10) forms the anterodorsal margin of the orbit and is sutured to the frontal, nasal and lachrymal bones. In addition, the supraorbitals, which are very well developed in this species, are attached to the ventral part of its lateral surface, on a slight boss. The ventral part of the orbital margin of the prefrontal is smooth and rounded; dorsally however, the margin is somewhat everted and rugose. The rugose area lies adjacent to the medial edge of the supraorbital, which is similarly rugose. Presumably the prefrontal and supraorbital were bound together by a sheet of connective tissue.

The broad, slightly concave base of the *supraorbital* (So. 1 - figs. 2, 3, 11) lies against the lower half of the external surface of the prefrontal. From its broad base (fig. 11 A, C) the main body of the supraorbital projects laterally for a short distance and then becomes sharply flexed backward and curves upward. Farther back, the supraorbital tapers gradually and becomes dorso-ventrally flattened (fig. 11 B, D). Posteriorly, the supraorbital ends in a blunt and rather irregular surface. The whole of the lateral and dorsal surfaces of the supraorbital are noticeably ridged and roughened (rug); the ventral surface, which lies immediately above the orbital cavity, is smooth and the medial surface is compressed to a sharp, rugose edge which lies adjacent to the lateral margin of the prefrontal and frontal. The basal portion of the supraorbital bears a slight lip along the posterior edge of its articular surface (art); this wrapped around the orbital margin of the prefrontal.

Immediately behind the supraorbital there is a small *Accessory supraorbital* (So. 2 - figs. 2, 3, 11); its irregular anterior surface tends to mirror that of the posterior end of So. 1 (fig. 11) and in all probability the two bones were held together by connective

tissue. Distally, So. 2 tapers gradually to a rounded point; its external surface is rounded and somewhat rugose, while its inner surface is flattened and rested against the adjacent postorbital. The surface of the postorbital of IRSNB. 1536, adjacent to So. 2, shows some evidence of moulding, perhaps suggesting that the supraorbital was held in position against the postorbital.

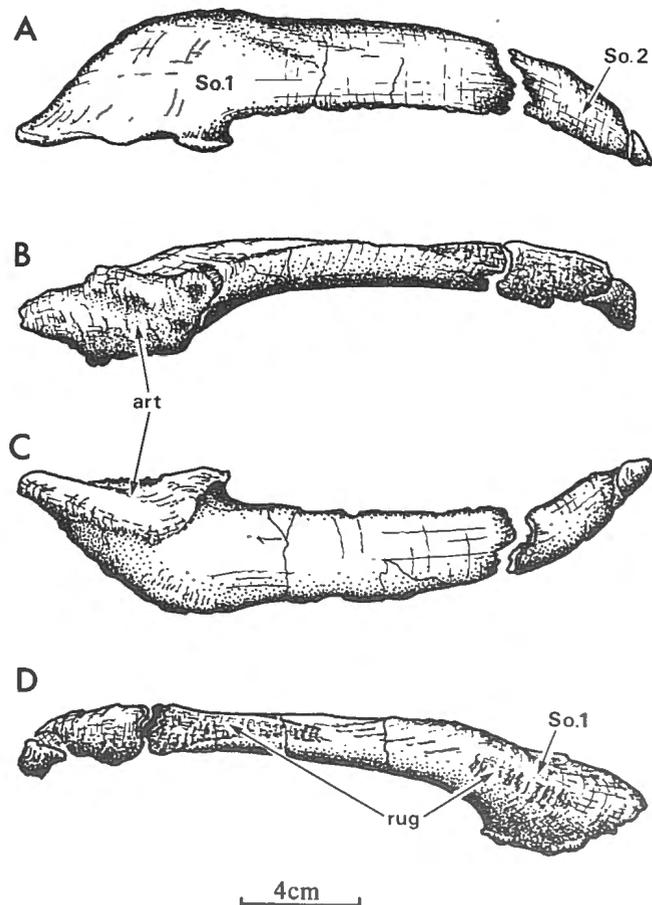


FIG. 11. — *Iguanodon bernissartensis*. (IRSNB. 1536). Right Supraorbital bones. A : dorsal view; B : medial view; C : ventral view; D : lateral view.

COOMBS (1972) speculated on the evolutionary significance of the supraorbitals found in all ornithischians (except hadrosaurs). In the discussion, his interpretation of the supraorbitals of *Iguanodon* was based on the original figures produced by DOLLO (1883). As a result COOMBS was rather misled about their position and appearance. He claimed, firstly, that the supraorbital articulated with both prefrontal and lachrymal and secondly, that the accessory supraorbital was an artefact resulting from *post-mortem* fracturing, quoting HOOLEY (1925) as evidence that *Iguanodon* had a single supraorbital, as is the case in most ornithopods. Both of these claims are incorrect. Incidentally, HOOLEY incorrectly identified the supraorbital in *I. atherfieldensis*; the bone which he described as « supraorbital » is the prefrontal.

The *postorbital* (Po - pls. 1-4; figs. 2-5) is a large T-shaped bone which partly separates the orbit from the temporal region of the skull. It contacts the frontal anteriorly and its suture with that bone extends from the margin of the orbit in a smooth curve inward and back (fig. 3) to meet the anterior extremity of the parietal and laterosphenoid along the front edge of the supra-temporal fenestra. From its anterior extremity, the main part of the postorbital extends horizontally backward to meet and overlap the squamosal, so forming the inter-temporal bar. From its ventral surface, the postorbital produces a forwardly curved, tapering process, which meets and overlaps the jugal, along the back edge of the orbit.

The *squamosal* (Sq - pls. 1-4; figs. 2-5, 9) forms the posterior dorso-lateral corner of the skull; it is a tri-radiate element connecting the braincase medially with the quadrate ventrally and the postorbital anteriorly. Medially, the squamosal meets several neurocranial bones; it overlaps the posterior end of the parietal dorsally, the supraoccipital posteromedially and wraps around the dorsal edge of the paroccipital process. It seems quite probable that a post-temporal opening passed through the occiput between supraoccipital and squamosal and opened out on to the lateral wall of the braincase (IRSNB. 1536, vcd - pl. 1; fig. 9). The contact between postorbital and squamosal has been described. The head of the quadrate fits snugly into a deep socket in the ventral surface of the squamosal (IRSNB. 1535); it is held in position by two processes, one in front and the other behind the quadrate head, and also by connective tissue which bound the quadrate head to the squamosal and otic region of the braincase. Above the quadrate cotylus, on the lateral surface of the squamosal, there is a prominent horizontal ledge which extends forward on to the inter-temporal bar; this ledge provided an area for attachment of superficial temporal jaw musculature (OSTROM, 1961).

The *quadrate* (Q - pls. 1-4; figs. 2, 5, 9, 12) together with the squamosal comprise the suspensorium, by which the lower jaw is braced against the braincase. The quadrate is essentially a pillar-like element, the anterior surface of which is modified into two thin diverging plates: a lateral one, the jugal wing and a medial or pterygoid wing.

The head of the quadrate (fig. 12 A, h), which sits in the squamosal cotylus, is smoothly rounded and triangular in dorsal view; its anterior border is somewhat excavated. The posterior edge of the quadrate descends vertically from the head for about one-third its total length, at which point it is interrupted by a shoulder-like buttress (fig. 12 A); beneath this, the border describes a very slight curve as it descends to the articular condyle for the mandible. The articular surface of this condyle is broad, rather more expanded laterally than medially (fig. 5) and saddle-shaped in anterior view.

The jugal wing (figs. 2, 13) is quite thin and describes an approximately convex curve anteriorly; originating from the antero-lateral corner of the head, it curves forward and downward. About mid-way down this wing there is a deep embayment for the quadrate/quadrate-jugal foramen (fig. 12 A, for). Beneath this recess the jugal wing converges on the main body of the quadrate, merging with it just above the distal condyle. The pterygoid wing is imperfectly known, but forms a deep plate which has an extensive overlapping suture with dorsal and ventral portions of a similarly deep plate of bone produced by the pterygoid. The ventral portion of this quadrate wing of the pterygoid appears to have been a thin and slightly hook-shaped process, which rests in a shallow groove along the medio-ventral edge of the pterygoid wing (fig. 12 C, pt.s). The dorsal portion of the pterygoid is separated from the ventral portion by a depression in the medial surface of the quadrate, above which it is attached to the internal surface of the quadrate. The dorsal part of the pterygoid wing of the quadrate can be seen through the lateral temporal fenestra (figs. 2, 13).

ming the anterior border of the quadrate/quadrate-jugal foramen. Its anterior surface bears a long vertical step against which the posterior surface of the jugal is sutured. Dorsally, the quadrate-jugal is produced into a long slender process with a groove running along its posterior edge; this groove fits against the anterior edge of the jugal wing of the quadrate. After spanning the quadrate foramen, the ventral part of the quadrate-jugal overlaps the ventral part of the jugal wing of the quadrate.

Passing forward along the jugal arch, the *jugal* (J - pls. 1-3; figs. 2, 4 A, 5, 13) is a large, flat bone linking the upper jaw with the suspensorium and forming the lower border to the orbit and lateral temporal fenestra. The jugal is attached to the maxilla by a tongue-in-groove articulation and contacts the lachrymal at its anterior extremity (from *I. mantelli*). Passing backward along its dorsal edge, the jugal forms the smoothly curved border to the orbit and extends upward as a rod-like process, which is triangular in cross-section and underlaps the ventral process of the postorbital. Posterior to this process, the upper edge of the jugal

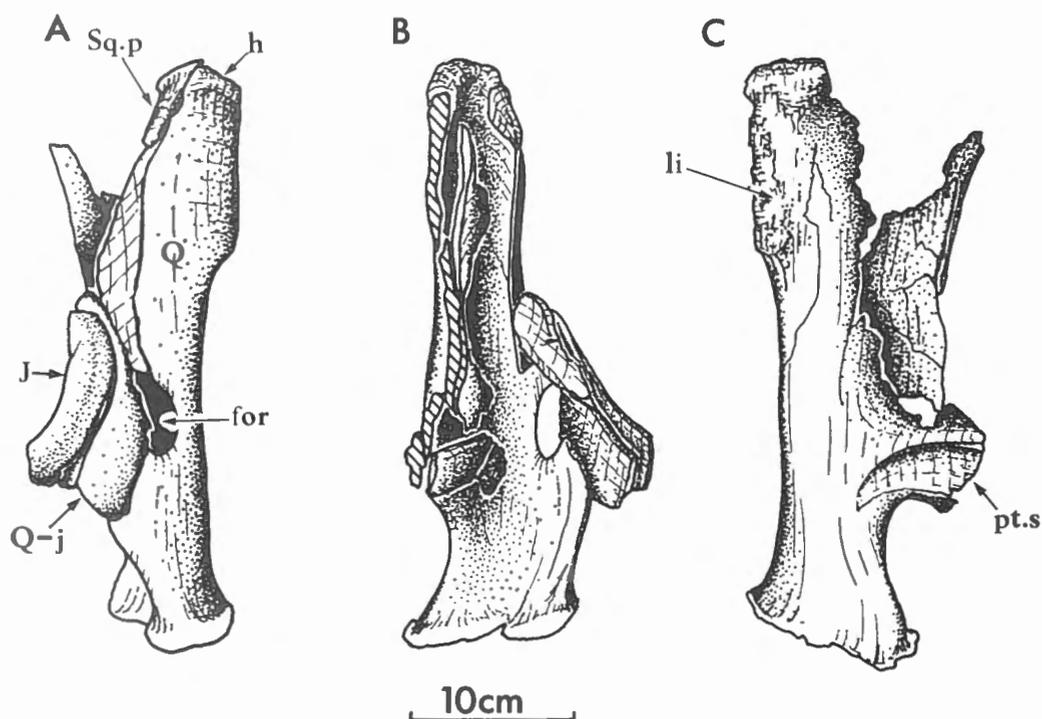


FIG. 12. — *Iguanodon bernissartensis*. (IRSNB. 1535). Left Quadrate and attached portions of the Jugal, Quadrato-jugal and pterygoid, as preserved.

The medial surface of the quadrate immediately beneath the head of IRSNB. 1535 (fig. 12 C, Li) appears quite noticeably scarred as if for attachment of connective tissue to the adjacent otic region of the braincase.

In many specimens, the *quadrate-jugal* (Q-j - pl. 1; fig. 2) is not at all well preserved. Nevertheless its principal features are seen in IRSNB. 1536 (fig. 13, Q-j). It consists of a relatively narrow flat plate of bone interposed between jugal and quadrate and for-

is deeply embayed, thus forming the U-shaped lower half of the lateral temporal fenestra. The posterior edge of the jugal lies against, and overlaps, the quadrate-jugal and tapers to a point at its upper end. The ventral edge of the jugal describes a sinuous curve and there appears to be a slightly thickened, rugose area posteriorly, which is probably homologous with the jugal « boss » noted in hadrosaurs (OSTROM, 1961) and *Heterodontosaurus* (CROMPTON and CHARIG, 1962).

(In *I. mantelli* the ectopterygoid articulates with the medial surface of the jugal.)

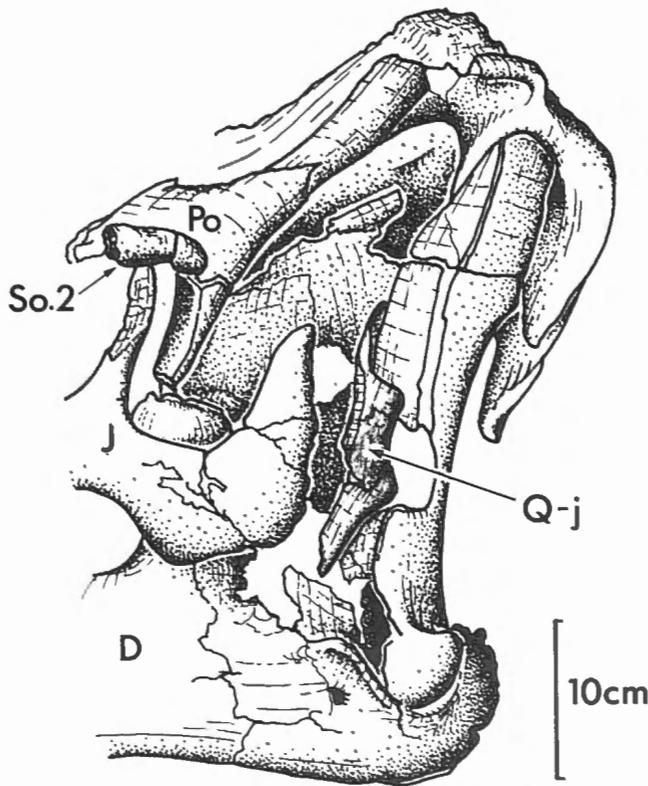


FIG. 13. — *Iguanodon bernissartensis*. (IRSNB. 1536).
Posterior portion of the left half of the skull.
Quadrato-jugal *in situ*.

Of the palatal elements, the vomers (V - fig. 9) are only poorly known in all species of *Iguanodon*. Fragments of vomer have been tentatively identified in IRSNB. 1561 and 1536 (pls. 2, 4). However, these are insufficient to provide for a description. The partial skull BMNH. R. 8306 (fig. 14) provides some evidence of the structure of the posterior part of the vomers.

From the evidence of the structure of the vomers in *Hypsilophodon* (GALTON, 1974) and *Brachylophosaurus* (HEATON, 1972) it can reasonably be assumed that the vomers contacted the median posterior extremities of the premaxillae (as indicated in fig. 9). From this contact they extend backward as gradually expanding, thin, vertical plates forming the medial walls to the nasal passages. The preserved portions of the vomers of BMNH. R. 8306 consist of the posterior halves. Each vomer is firmly sutured to its neighbour along its ventral edge (fig. 14, cross-hatched area); this edge runs more or less horizontally at approximately the same level as the top edge of the internal surface of the maxilla, ending as a point posteriorly roughly level with the antorbital foramen (fig. 9). From this posterior end, the edge curves upward, outward and backward as the two vomers diverge and produce long style-like processes which may have articulated with the ptery-

goids (fig. 14). From these pointed extremities, the upper edge of each vomer extends forward along the roof of the nasal passage and curves downward anteriorly to meet the premaxillae.

Presumably the gap between the keel-like ventral edge of the vomers and the maxillae laterally was spanned by sheets of connective tissue forming a soft palate separating nasal and buccal cavities.

Behind and on either side of the vomers, the palatines (Pal - pls. 1, 3, 4; figs. 2, 9, 10) are rhomboid curved plates, forming the lateral wall and arching over to roof the nasal passages, medial to the orbital cavities. Each palatine is sutured to the postero-dorsal edge of the maxilla and is supported behind by a narrow ascending palatine ramus of the pterygoid. The palatine of *Iguanodon* is quite similar in general shape to that of the flat-headed hadrosaur *Edmontosaurus* (LAMBE, 1920).

The pterygoids (Pt - pls. 1-4; figs. 5, 8, 9, 14) are perhaps the most complex of the skull bones. Unfortunately, they are also among the most poorly represented. The pterygoid of *Iguanodon* illustrated here is a composite reconstruction based upon the various fragments which are presently known (IRSNB. 1536, 1561 and BMNH. R. 8306), along with knowledge of the construction of the pterygoid of the reasonably closely related flat-headed hadrosaur *Edmontosaurus* LAMBE, 1920; HEATON, 1972.

The pterygoid is the key element in the palatal complex and is basically a central plate from which radiate three rami of varying shape. These rami serve to link the anterior bones of the palate with the braincase, suspensorium and upper jaw.

The anterior projection or palatine ramus of the pterygoid is long, narrow, projects obliquely forward and upward, and is sutured along the sloping posterior edge of the maxilla (fig. 9); this suture is continuous with its oblique suture to the palatine. The distal tip of this ramus appears to back on to the distal tip of the vomer (fig. 14) and in so doing, becomes twisted inward (fig. 5, 9) producing a curved ledge immediately behind the palatine. Passing backward along this ramus, the internal ledge becomes broader, forming a curved plate of bone roofing the back of the nasal passage (fig. 14, m.fl). The medial and dorsal parts of the proximal end of the palatine ramus and most of the central plate of the pterygoid are not well preserved in any of the specimens. The important region of the pterygoid which provided for the basal articulation therefore remains at present unknown (i.e. dotted area, figs. 4 B, 5, 9).

Below the area of the basal articulation, adjacent to the posterior end of the maxilla, there is an oblique backwardly directed process of the pterygoid, the ectopterygoid ramus (Ec. p - figs. 5, 18, 14). Laterally, it forms a thickened process, which is overlapped by the ectopterygoid. Medial to this process its dorsal surface forms a broad, shallow trough, running obliquely for-

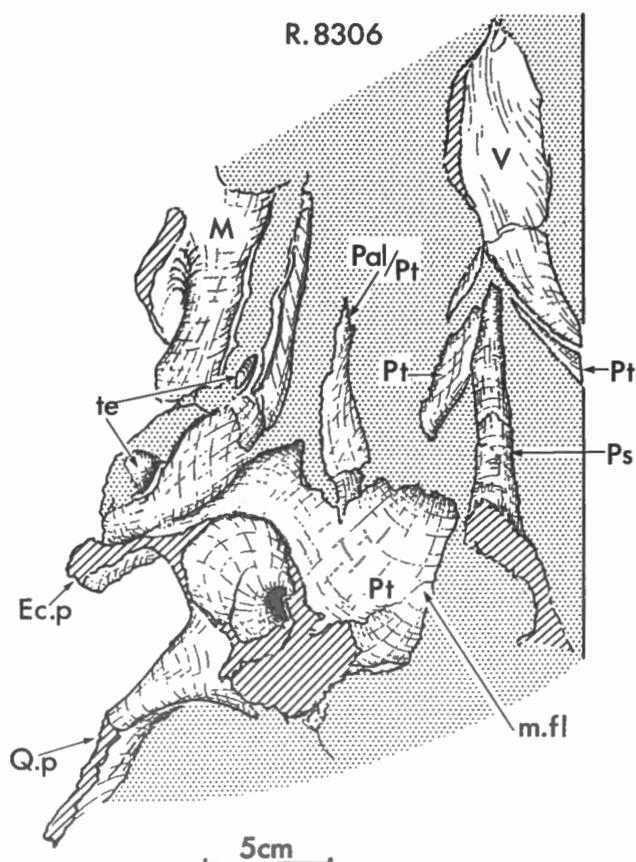


FIG. 14. — *Iguanodon bernissartensis*. (BMNH. R. 8306).
Ventral view of the palatal region of a partial skull.
Even stippling indicates matrix, cross-hatching indicates broken bone surface.

ward and upward behind the maxilla (fig. 8). Medially, this trough is bounded by a low ridge, which arises from the distal tip of the medial edge of the ectopterygoid ramus and curves forward and upward to meet the ventral edge of the quadrate ramus of the pterygoid. Medial to this ridge there is another, although smaller, trough-like depression, which extends forward beneath the approximate position of the basal articulation and is bounded by the medial edge of the pterygoid (figs. 5, 8).

Above the ectopterygoid ramus, the *quadrate ramus* (Q.p) of the pterygoid is a two-pronged, thin vertical plate of bone, which forms an extensive overlapping suture with the quadrate. The ventral « prong » of this ramus is elongate and narrow, and rests in a shallow groove along the medio-ventral margin of the pterygoid wing of the quadrate (figs. 8, 12 C, pt.s). The dorsal « prong » is more wing-like and overlaps the more dorsal part of the inner surface of the quadrate (see fig. 4 B).

Lying across the postero-lateral surface of the maxilla is a small, thin, strap-like ectopterygoid (Ec - pl. 3; fig. 5). In *I. mantelli*, it lies in a shallow trough in the maxilla and contacts the medial surface of the jugal with its anterior extremity. In *I. bernis-*

sartensis, this bone is visible in a few instances and is indistinguishably fused to maxilla and pterygoid. An apparent roughening of its external surface in IRSNB. 1536 suggests that it may have provided part of the area for attachment of *M. pterygoideus dorsalis*.

The Mandible.

The *prementary* (Pd - pls. 1, 2; figs. 2, 5, 9, 15) is the only unpaired mandibular bone, being a median, scoop-shaped crescent of bone, which reinforces the dentary symphysis. It undoubtedly supported a horny beak along its edentulous occlusal margin. In dorsal view (fig. 15) the occlusal margin is smoothly curved; anteriorly, this margin bears several large, conical, bony projections which become less prominent laterally where they form merely an irregular edge. These structures undoubtedly supported the lower horny beak and also probably influenced its structure. Numerous vascular foramina open on to occlusal surface of the prementary (fig. 15, v.for) presumably supplying nutrients to the growing area of the beak. In lateral view (fig. 2) the curved outer surface of the prementary is wedge-shaped, the lower border rising to meet the upper border posteriorly. The posterior process, on either side, has a notch into which the dentary fits (fig. 15). From the ventral midline there is developed a large, flat, bilobed structure, the two lobes of which are attached to the ventral surface of the dentaries on either side of the symphysis. The short median stalk, which supports these lobes, sits between two short prongs produced by each dentary just anterior and lateral to the symphyseal region.

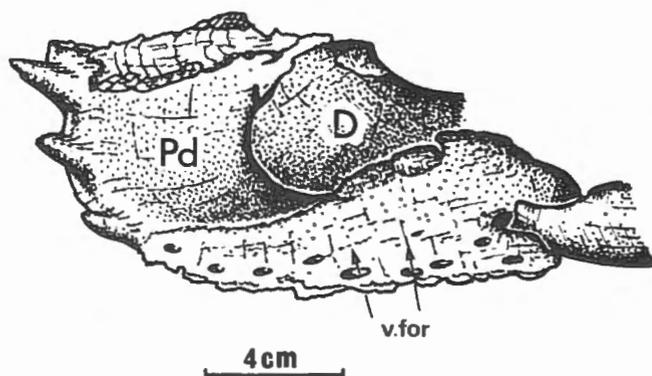


FIG. 15. — *Iguanodon bernissartensis*. (IRSNB. 1561).
Prementary. Dorsal view of left half, as preserved,
articulated with the Dentary.

In hadrosaurs (OSTROM, 1961 : fig. 17 a) there is a median dorsal process of the prementary which serves to clamp the prementary above the symphysis. A similar process is suspected in *Iguanodon*, but none has so far been found.

The anterior end of the *dentary* (D - pls. 1-4; figs. 2, 5) tapers to a rounded projection along its

ventral border, just behind and medial to which is the horizontal symphyseal suture (sym - fig. 9). The upper edge of the dentary curves smoothly upward and backward and against this surface the prementary is attached; immediately below this border there is a series of large vascular foramina (fig. 2). Behind the prementary suture, the dorsal border of the dentary passes horizontally backward as a neatly scalloped alveolar border, supporting the functional teeth. Medially, the teeth are retained by a rather thin alveolar parapet (Ap - pl. 2; fig. 9); its surface texture and vascular supply are identical to that already noted on the maxilla.

Passing backward from the area of the first alveolus, the dentary becomes increasingly thick, when viewed from above (pl. 4) until it reaches the coronoid process. As in all advanced ornithischians, the tooth rows are aligned along the medial edge of the dentary, so that a shelf develops between the alveolar margin and the lateral wall of the dentary. The floor of this shelf bears several large foramina which are branches from a large canal which runs just beneath the shelf (BMNH. R. 28660). The functional teeth run in a straight line for most of their length but, as they approach the coronoid process, curve outward, toward its base (pl. 4). Below the alveolar parapet on the medial side, there is an elongate groove, the Meckelian canal (pl. 2, Me); this is shallow anteriorly, but becomes deeper posteriorly and opens out into the mandibular (adductor) fossa (pl. 4, ad.f). There is a long, shallow depression on the dentary just above the Meckelian canal, which marks the area for attachment of the prearticular (see pls. 2, 4).

The posterior end of the dentary is somewhat complicated to allow firm attachment of the remaining mandibular bones. The coronoid process is prominently marked over its medial surface by oblique striations and ridges for attachment of the coronoid

bone. The posterior surface of the coronoid process is sharp-edged and overlaps the surangular (pl. 3). Below the hindmost alveoli, the medial surface of the dentary is developed into a thin backwardly directed process (pl. 2, pr); this borders the mandibular fossa medially and supports the prearticular.

Attached to the medial side of the coronoid process is found the *coronoid* bone (Co - pls. 1-4). This is a small, flat, kite-shaped bone, most of the lateral surface of which is firmly sutured against the coronoid process of the dentary. It extends above the dorsal margin of the coronoid process so as to be partly visible in lateral view (pls. 1, 3). The dorsal edge is smoothly curved and somewhat rugose and descends posteriorly to lie against a narrow ascending process from the surangular. The anterior border of the coronoid descends, just behind the leading edge of the coronoid process, curving postero-medially toward its base and apparently terminating just behind the last alveolus (pls. 1, 4).

Behind and below the coronoid, the *surangular* is attached to the dentary by an extensive overlapping suture (Sa - pls. 1-4; fig. 2). While the lower half to the dentary-surangular suture is relatively simple, the dentary overlapping the surangular, the dorsal part is rather more complex, with the surangular developing a lip which overlaps the dentary and farther dorsally develops a process which fits into a recess in the posterior border of the coronoid (see pl. 1).

From the coronoid above, the posterior border of the surangular descends steeply to the glenoid. The glenoid is large and bowl-shaped, the major part of which is formed of surangular (pl. 4; fig. 16, gl). The lateral margin of the glenoid is thickened and everted just above the large surangular foramen (fig. 2). Internally, the dorsal border of the surangular descends steeply and curves inward, forming the postero-lateral border to the mandibular fossa (fig. 16 B), and ending

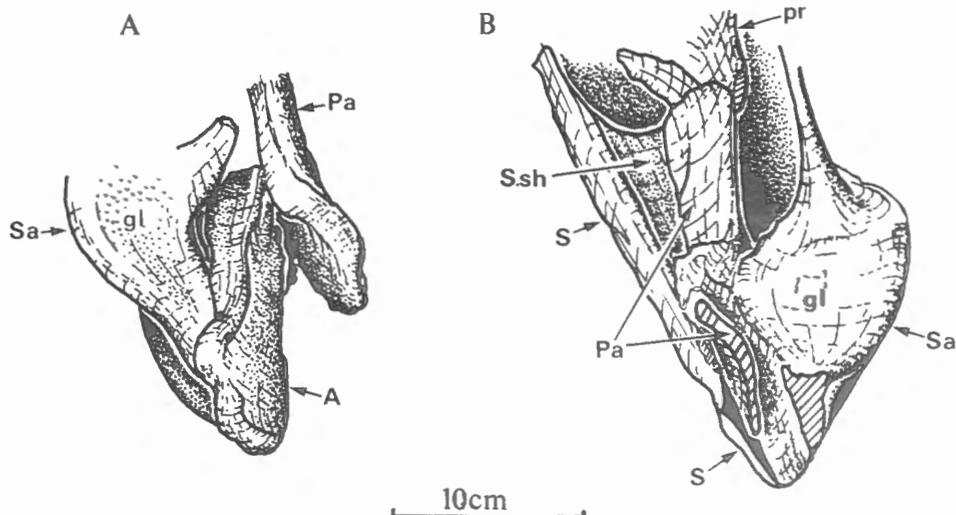


FIG. 16. — *Iguanodon bernissartensis*. Posterior view of the hind end of the lower jaw. A: IRSNB. 1561; B: IRSNB. 1536.

as a short, blunt medial process (fig. 16 A). Behind this process there is a longitudinal recess in the medial surface of the surangular against which the articular is sutured. Posteriorly, the outer and inner sides of the surangular converge in an upturned lateral portion of the retroarticular process. The lateral surface of the surangular, just beneath the retroarticular process, is often scarred for the insertion of *M. pterygoideus ventralis*.

Ventrally, the surangular has a long, shallow recess from the base of the retroarticular process forward to the dentary; this received the splint-like angular bone.

The thin, splint-like *angular* (An - pl. 3; fig. 2) contacts the dentary anteriorly, the prearticular mesially, the surangular and possibly the articular dorsally.

The *articular* (A - pls. 1, 2; figs. 9, 16) is wedged into the posterior of the mandible between prearticular and surangular. Its exact form is unknown because in all specimens it has been damaged or lost. Specimen IRSNB. 1561 (fig. 16 A) shows some evidence of the presence of the articular. It appears to have been a relatively narrow strip of bone with a thickened dorsal edge which formed the internal edge of the glenoid. Below the dorsal surface, the lateral surface of the articular rested in a horizontal recess in the surangular and its medial surface was overlapped by the prearticular. Posteriorly, the articular appears dorso-ventrally expanded and formed the medial part of the retroarticular process.

The *splénial* (S - pls. 2, 4; figs. 9, 16) is a thin plate of bone lying over the lower half of the prearticular and forming the medial wall of the Meckelian canal. It produces a shelf (fig. 16, S. sh) at its posterior end, which runs across the floor of the adductor fossa toward the surangular. It appears to terminate between prearticular and angular posteriorly; however, its anterior limit is unknown, although it probably extended beyond the prearticular and approached the symphysis.

The *prearticular* (Pa - pls. 2, 4; figs. 9, 16) is a thin sheet of bone forming the medial edge of the mandibular fossa. Anteriorly, it forms an elongate thin sheet which lies against the internal surface of the dentary, beneath the alveolar parapet, and is overlapped by the splénial. Posteriorly its dorsal edge curves upward, producing a narrow process beneath the coronoid process. Posterior to this dorsal process, the dorsal border curves downward and backward around the mandibular fossa. The prearticular terminates posteriorly, adjacent to the articular and splénial and medial to the glenoid.

Accessory Skull elements.

Sclerotic Ossicles. — In none of the preserved skulls of *I. bernissartensis* is there any evidence of a bony sclerotic ring in the orbit. This apparent absence seems extraordinary, as possible ancestors

and descendants of *Iguanodon* — the hypsilophodontids and hadrosaurs respectively — possess well-developed sclerotic rings (GALTON, 1974; EDINGER, 1929; OSTROM, 1961 and RUSSELL, 1940). Most probably, *Iguanodon* possessed sclerotic bones but these have so far not been discovered.

Hyoid apparatus. — The only preserved parts of the hyoid apparatus are the paired bones which have been found lying between the mandibles in several of the Bernissart specimens. Each bone (fig. 17) is an elongate, curved rod, which is expanded and abruptly truncated at its anterior end, while tapering to a narrower but also blunt posterior end.

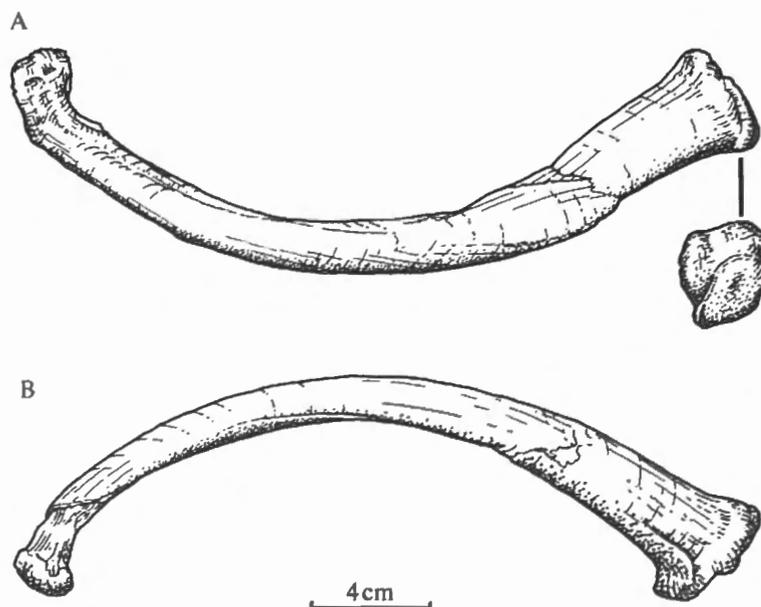


FIG. 17. — *Iguanodon bernissartensis*. (IRSNB. 1561).

In the skull of the generalised iguanid lizard *Ctenosaura* (OELRICH, 1956), the paired first ceratobranchials occupy a position between the mandibles almost identical to that of the « hyoid » bones of *Iguanodon*. In addition, not only are the first ceratobranchials of *Ctenosaura* closely similar in shape to those of *Iguanodon*, but they are also the most highly ossified of the hyoid elements — therefore, in theory the most likely to be preserved during fossilisation. Although these links are admittedly tenuous, it is suggested that the hyoid bones of *Iguanodon* are probably first ceratobranchials. The absence of any well-developed articular surface on the anterior end of the first ceratobranchial of *Iguanodon* may be explained by the presence of a capping of hyaline cartilage similar to that in *Ctenosaura*; this provides for articulation between this bone and the main body of the hyoid.

Similar hyoid bones have been found in many ornithomimid dinosaurs: *Hypsilophodon* (GALTON, 1974); *Camptosaurus* (GILMORE, 1909); *Ouranosaurus* (TAQUET, 1976); *Corythosaurus* (OSTROM, 1961), etc.

Dentition.

The teeth of *Iguanodon* are arranged in a longitudinal series of vertical rows in both upper and lower jaws. The number of vertical rows in both jaws differs even though the tooth batteries are of the same length: the maxillary teeth are narrower than the dentary teeth, so that a few (3-4) more rows are usually present in the upper jaw. The maximum number of vertical tooth rows in the maxilla appears to be 29 (IRSNB. 1536) with 25 in the dentary.

The maxillary and dentary teeth are readily distinguishable and are therefore described separately. Though various terms have been used by palaeontologists in describing the morphology of teeth, to avoid confusion the terms used in this description are related to the orientation of the mandible, rather than to their orientation relative to the buccal and lingual cavities. This has proven possible because, fortunately, the teeth are confined to the cheek region of the jaws alone. « Anterior », « posterior », « medial » and « lateral » are therefore unequivocal terms referring to the orientation of each tooth relative to the long axis of the skull.

Dentary teeth. — (Figs. 18, 19 — The teeth in fig. 18 correspond to those indicated by letters in fig. 19). These teeth possess long tapering roots, which curve medially as they arise from their origin in the base of the alveolus. The anterior and posterior sides of the root bear shallow, concave, vertical grooves, which end just beneath the widest part of the crown (fig. 18 A, B). The edges of adjacent tooth crowns fit against these grooves, so producing a partly interlocking battery of teeth (fig. 19).

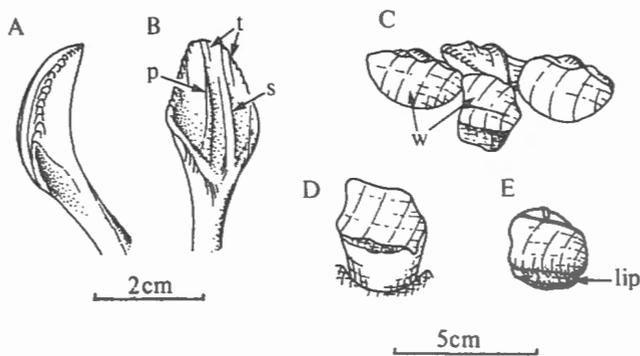


FIG. 18. — Selected dentary teeth. A, B: anterior and medial views of an anterior dentary tooth as indicated in fig. 19. C: occlusal view of teeth indicated in fig. 19. D, E: lateral and occlusal views of teeth as indicated in fig. 19.

The crown is broadly expanded antero-posteriorly and is roughly leafshaped in medial view (fig. 18 B); this surface is covered by a thick layer of enamel, which in turn is ornamented by several vertical ridges and fringed by marginal denticles. Laterally, the main body of the crown consists of dentine, is concave vertically

and convex antero-posteriorly. The medial and lateral surfaces meet at an acute angle, forming the serrated dorsal margin.

The base of the crown is supported by two thickened, divergent shelves of enamel, which merge anteriorly and posteriorly into the lower edge of the denticulate border. The marginal denticles, in turn, consist of short crests of enamel which wrap around the edges of the crown; they are also graded in size, being smallest near the apex of the crown, and largest down the sides of the crown.

The pattern of vertical ridges which run down the enamelled face of the crown is reasonably characteristic. The dominant feature is a large *primary ridge* (fig. 18 p) which divides the surface into two unequal halves. The smaller posterior portion is bounded by the marginal denticles and the shelf region below. This surface is usually devoid of subsidiary ridges, although one or two small ridges may extend downward across this surface from the base of some of the denticles. The larger anterior area of the crown is further subdivided by a *secondary ridge* (fig. 18 s) which is broader and not so well-defined as the primary ridge. Various *tertiary ridges* (fig. 18 t) may be present and are quite variable in their distribution on the crown surface, even within a single dentition. They are usually short, narrow ridges, which arise from the bases of the marginal denticles, especially along the dorsal part of the crown edge; they can also on occasions arise from the secondary ridge itself.

A pattern of transverse bands, or fluting, can often be seen in the enamel of the teeth of both upper and lower jaws and has the superficial appearance at least of growth bands.

Within the lower dentition, the teeth show some variability in size and in overall shape. Anteriorly, the teeth are small and lanceolate (fig. 19) while posteriorly they become progressively larger and broader, reaching a maximum size just posterior to the middle of the dental series; at the hind end of the series the teeth become smaller but are less pointed than the anterior ones.

Maxillary teeth. — (Figs. 20, 21). Like the lower ones, the upper teeth have long, tapering, curved roots, the anterior and posterior sides of which are deeply grooved to receive the crowns of adjacent teeth (fig. 20A). The crowns of the upper teeth are much narrower than those of the lower teeth and the arrangement of enamel ridges is clearly distinct. Large, curled shelves are present along the bases of the anterior and posterior edges, and from these the denticles develop; they extend laterally on to the external surface of the crown to a greater degree than in the lowers.

The enamel surface of the crown faces laterally, not medially as in the lower crowns. The enamelled face is divided unequally by a very prominent, narrow primary ridge (fig. 20 B, p). As with the lower teeth,

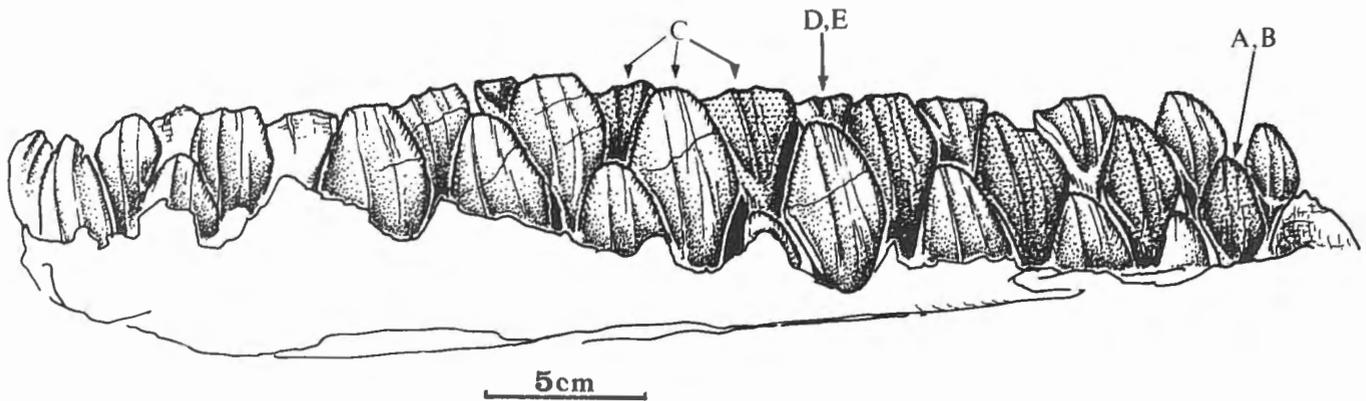


FIG. 19. — *Iguanodon bernissartensis*. (IRSNB. 1561). Dentition of the left lower jaw, as preserved. Replacement « wave » indicated by even tone.

this ridge separates the broader anterior from the posterior part of the crown. The posterior portion forms a narrow valley between the primary ridge and the raised denticulate border and is usually traversed by one or two small tertiary ridges (fig. 20 B, t). The anterior portion of the enamelled surface is not subdivided by a secondary ridge as it is in lower teeth, but instead forms a low flat surface traversed by several tertiary ridges.

duced and also to cope with the limitations imposed by the lack of space for replacement crowns in both upper and lower jaws.

In the lower jaw the alternate arrangement and staggered eruption sequence allows the diamond-shaped tooth crowns to interlock. Thus, each tooth contributes, and is provided with, support in addition to that provided by the alveolar bone.

Each functional tooth has a single replacement crown below it (fig. 19). The replacement first develops as a small crown in a position just medial to the root of the functional tooth. As growth progresses, the replacement crown occupies an increasing proportion of the space available within the alveolus. Consequently, during later phases of eruption, the replacement crown stimulates resorption of the medial part of the root of the functional tooth. This process continues until the functional tooth has been reduced to a short stump which then falls from the jaw.

The upper jaw is far narrower than the lower jaw and, as a consequence, tooth replacement is slightly different (fig. 20). The replacement crown (r.c.) grows directly beneath the functional tooth in a notch (re), so that subsequent growth causes almost complete resorption of the functional tooth root from beneath rather than medially as in the lower teeth, leaving a rootless stump which falls from the jaw.

Tooth Wear. — During mastication the teeth become worn to produce an oblique medio-dorsal/latero-ventral occlusal plane. The worn surfaces of the upper and lower teeth (w - figs. 18, 20) therefore form trenchant, chisel-like cutting edges, which slope steeply away from the hard, enamelled edges to the softer dentine. The interlocking teeth form a continuous cutting edge along each jaw (pls. 1-4). The cutting action of the teeth is enhanced by the irregular nature of the enamel edges to the worn teeth; this is particularly apparent with the maxillary teeth, in which the primary ridge of each tooth forms a particularly prominent, jagged, cutting surface (fig. 20 A).

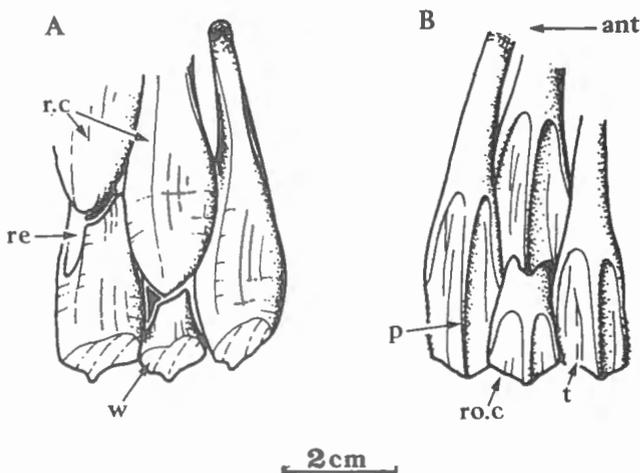


FIG. 20. — *Iguanodon* sp. (BMNH. R. 40100). Selected maxillary teeth, demonstrating replacement process *in situ*.

Tooth Replacement. — The replacement sequence is typically reptilian, consisting of alternate waves of replacement which pass forward along the dental series. A complete wave of replacement of dentary teeth occupies between 8 and 9 alternate tooth positions, from rudimentary crown anteriorly, to a worn stump in the process of being shed posteriorly (fig. 19, shaded series), while in the maxilla a replacement wave consists of 4 or 5 alternate tooth positions (fig. 21). The replacement strategy has been slightly modified to enable a rudimentary battery to be pro-

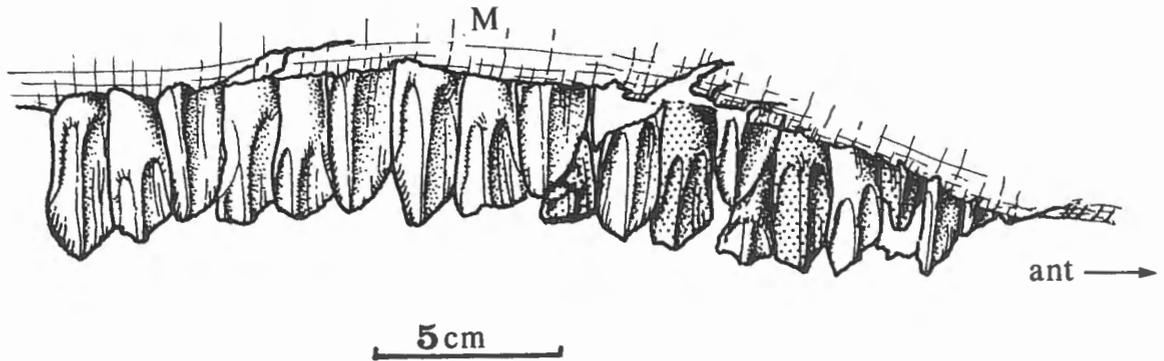


FIG. 21. — *Iguanodon bernissartensis*. (IRSNB. 1536). Maxillary dentition, anterior portion, as preserved. Replacement « wave » indicated by even stippling.

THE VERTEBRAL COLUMN.

Although there is abundant vertebral material of this species, none is preserved as a complete, articulated vertebral column. Composite restorations have therefore been produced and these are supplemented by various examples of isolated representative vertebrae, in order to illustrate additional salient characters and to give an idea of the general preservation of the material.

Cervical Vertebrae.

There are eleven cervical vertebrae in *I. bernissartensis* (fig. 22) and there is probably also a pair of

proatlases (p. at) as found in the closely related species *I. mantelli*.

The atlas (at - figs. 22, 23) consists of an intercentrum, odontoid and two neural arches. The intercentrum (ic. 1) is a crescent-shaped strip of bone, which bears along its anterior edge a broad, shallow, concave depression, that articulates against the occipital condyle (fig. 23 d, oc.a); the ventral edge of this articular surface is thickened. Above and behind this articular surface, there is a smooth, transversely concave bar which receives the ventral edge of the odontoid. On either side of this bar there are two shoulders which have rugose dorsal edges; these serve as areas for attachment

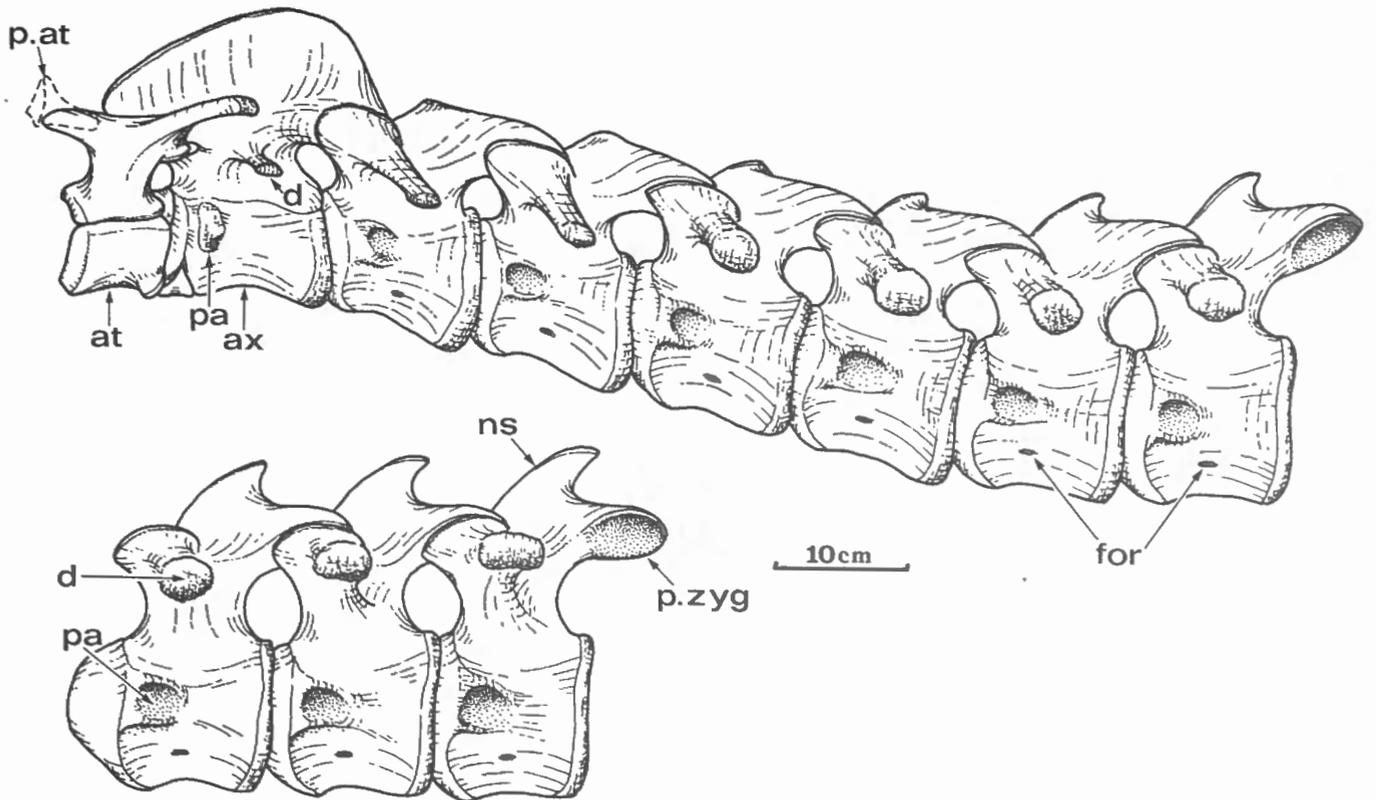


FIG. 22. — *Iguanodon bernissartensis*. The articulated cervical vertebrae. Based on IRSNB. 1536, 1561.

of the pedicels of the neural arches. The posterior surface of the intercentrum is convex vertically, more or less flat transversely and rests against the antero-ventral surface of the axis and its intercentrum. The ventro-lateral corners of this surface are produced into small flap-like projections (r), these are concave posteriorly and each receives the single head of the atlantal rib. Ventrally, the surface of the intercentrum is rounded transversely, with a slight depression between the anterior and posterior margins.

The *odontoid* (od) is well preserved in several specimens. It is firmly sutured to the centrum of the axis (fig. 24 a) and from this broad flattened base, it projects forward horizontally as a dorsally flattened cylinder. The lateral and ventral sides are slightly contracted along their length, as they run over the cradle formed by the atlas intercentrum. At its distal end, the odontoid is slightly expanded and obliquely truncated; this flattened end lies approximately flush with the articular surface for the occipital condyle. The dorsal surface is flattened to form the floor of the neural canal.

The *neural arches* (na - fig. 23) are fused neither to each other nor to the intercentrum. Their pedicels are expanded antero-posteriorly and rugose ventrally; the rugosities indicate that they were attached by connective tissue to the shoulders of the intercentrum. The anterior end of each pedicel is modified into a shallow concave articular facet (fig. 23 d, oc.a) which faces obliquely forward and downward and articulates with the occipital condyle. Above their bases, the neural arches contract and curve upward and inward to enclose the neural canal. Anteriorly, each arch is developed into a thin, curved prezygapophysis, which overhangs the occipital condyle and undoubtedly supported a proatlas. The posterior edge of the neural arch is developed into a tapering postero-laterally directed spine, or transverse process. Medial and anterior to this spine, the medial edge of the roof of the neural arch faces its neighbour; the posterior half of this edge is recessed on each side so that together they form a broad notch into which the enormous neural spine of the axis is able to fit. On the ventral

surface of each arch, adjacent to this recessed margin, there are found the broad, shallow depressions of the postzygapophyseal facets (fig. 23 c, p.zyg.).

The *axis vertebra* (fig. 22 ax; 24) is considerably larger than the atlas, bearing an enormous neural spine upon a cylindrical and strongly opisthocelous centrum (fig. 24). Anteriorly, the surface of the centrum which articulates against the atlas is complex: the dorso-medial region forms a flattened plate to which the odontoid is sutured; immediately beneath this, there is a curved area to which is sutured the small crescent-shaped wedge of bone, the axis intercentrum (ic.2). The latter forms a slight lip along the antero-ventral edge of the axis, underlapping the atlas intercentrum when atlas and axis are in articulation (fig. 22).

The centrum of the axis is expanded at both ends and contracted about its middle. The ventral surface is rounded and does not bear the thick keel which is so well developed in succeeding cervicals (the « keel » in fig. 24 c is an artefact produced by crushing). Midway up the side of the centrum, just behind the everted anterior articular margin, there is a small flattened apophysis: the parapophysis for the capitulum of the axis rib (fig. 22 ax, pa).

The neural arch supports and is dominated by the enormously expanded neural spine. The prezygapophyses are unusual in that they face antero-laterally instead of medio-dorsally as in the remaining cervicals. Extending forward as a large hook-shaped vertical plate between the prezygapophyses is the anterior extremity of the neural spine; from this extremity, its dorsal edge curves upward and backward as a thin blade; the apex is situated vertically above the posterior margin of the centrum. From the apex, the neural spine divides into two buttresses which diverge and descend quite steeply to form the large ventro-laterally directed postzygapophyses. Between pre- and postzygapophyses along each side of the neural arch, there is a narrow ledge which produces a short, stout, ventro-laterally directed transverse process which supports, at its truncated end, a small rib diapophysis (fig. 22 d).

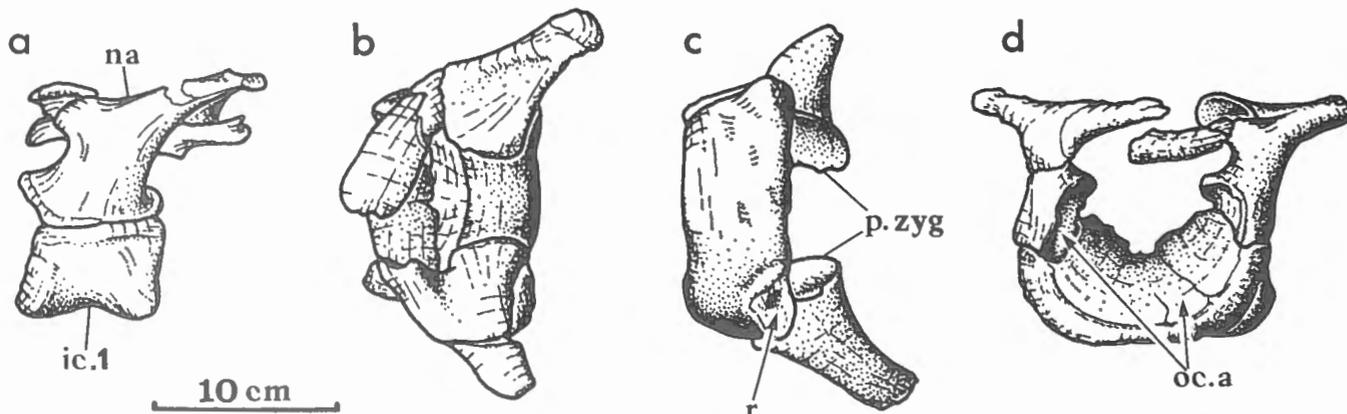


FIG. 23. — *Iguanodon bernissartensis*. (IRSNB. 1561). Atlas vertebra as preserved. a: lateral view; b: dorsal view; c: ventral view; d: anterior view.

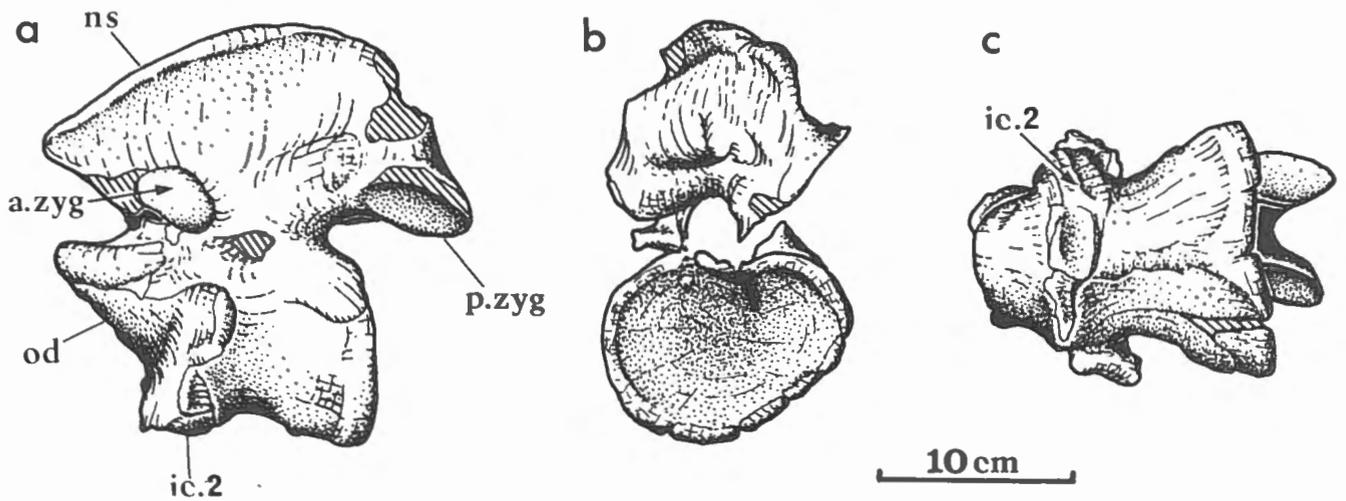


FIG. 24. — *Iguanodon bernissartensis*. (IRSNB. 1561). a : lateral view; b : posterior view; c : ventral view.

All the centra of the remaining cervical vertebrae are strongly opisthocoelous and possess correspondingly large hemispherical, anterior articular surfaces (figs. 22, 25, 26). The latter are not entirely regular, since they usually possess a slight notochordal pit at their centre. Ventrally the centra are transversely compressed so producing a thick, rounded, rugose keel; this is narrowest anteriorly, just behind the margin of the anterior articular condyle, and widens posteriorly as it gradually merges with the posterior margins of the centrum (fig. 26, b, k). Above the keel, the lateral walls are concave and usually pierced by a small round foramen (fig. 22, for). At the middle of the centrum there is a horizontal ridge which possesses a low, rectangular parapophysis anteriorly (p). Above this

ridge, the sides of the centrum are again contracted as they sweep inwards and upwards into the neuropophyses.

The neural arch is quite a complex structure in the cervical series; it forms a wide arch above the neural canal, which is anchored to the centrum by stout neuropophyses. From the outer surface of the arch, there are developed two paired processes: the lower, more anteriorly placed transverse processes, which support the large prezygapophyses as well as the diapophyses; and, the large curved postzygapophyses, which arise from the midline above and between the transverse processes, diverging as they curve upwards and backwards to terminate at their zygapophyseal facets.

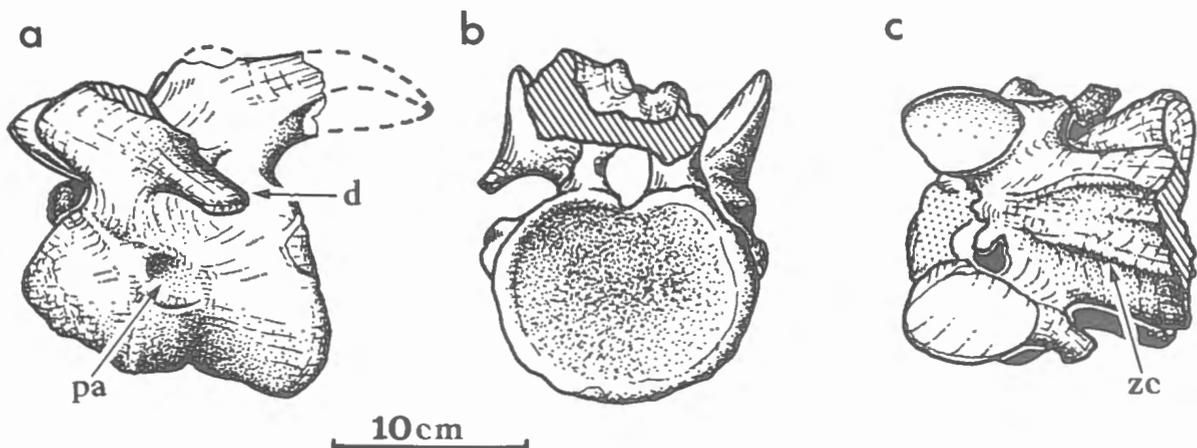


FIG. 25. — *Iguanodon bernissartensis*. (IRSNB. 1561). 3rd Cervical vertebra, as preserved. a : lateral view; b : posterior view; c : dorsal view.

The parapophyses of the cervical series are sub-rectangular depressions situated immediately behind the articular margin of the anterior surface of the centrum, about mid-way up the side of the centrum. The neurocentral suture, although rather obscured in most cases, lies above the parapophysis in all the cervicals. The parapophysis of the more posterior cer-

vicals is larger and positioned higher on the side of the centrum, heralding the change from cervical to dorsal vertebral morphology and also revealing the adaptations for carrying a larger rib.

Progressing along the cervical series, a number of gradual changes in structure can be observed (fig. 22). In the anterior region, the centra are quite low, slightly

dorso-ventrally compressed cylinders (fig. 25); however, farther posteriorly they become broader and especially deeper, so that they become by stages transformed into the deeper, laterally compressed form of the succeeding dorsal series. The neural spine (ns) is virtually absent in the anterior part of the series, being represented by small ridges (zc) at the base of each postzygapophysis (fig. 25 c). However, farther along the series the spine develops from a low crest into a prominent hook-shaped blade (fig. 22). The prezygapophyses, are at first large forwardly directed processes overhanging the preceding centrum (fig. 25 a, c). In later members of the series, they become less prominent and retreat on to the dorsal surface of the now larger and laterally directed transverse processes (fig. 26 c). The transverse processes at first form mere forwardly directed oblique processes, supporting the large prezygapophyses, with rudimentary postero-ventrally directed diapophyses (fig. 25). Subsequently, as the prezygapophyses retreat and the ribs enlarge, the transverse processes become considerably larger, develop buttressing ridges beneath, and laterally directed (fig. 26). The diapophyses become larger and higher to support the larger posterior cervical ribs.

the hind end of the series, the curvature of the neck is reversed; this is achieved by exactly the reverse of the previous modifications, of which the proportionate antero-posterior shortening of the neural arch is especially obvious in this respect.

Cervical Ribs.

The *atlantal rib* appears to have been consistently confused with the hyoid bone, and *vice versa*, in the

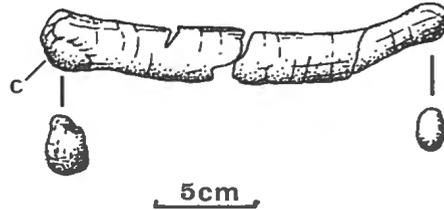


FIG. 27. — *Iguanodon bernissartensis*. (IRSNB. 1561). Atlas rib (right) medial view.

Bernissart collections. Typically, the atlantal rib is a single-headed, elongate, laterally compressed rod (fig. 27). Its head (c) is slightly expanded and fits against

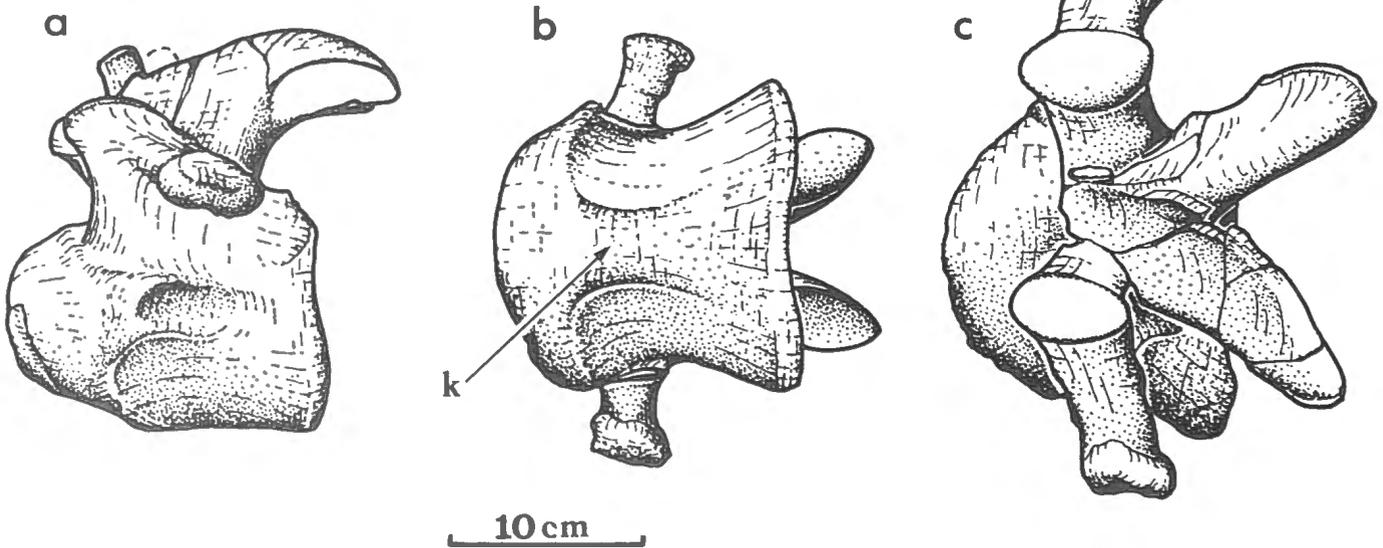


FIG. 26. — *Iguanodon bernissartensis*. (IRSNB. 1561). 6th Cervical vertebra, as preserved. a : lateral view; b : ventral view; c : dorsal view.

When the cervical series is naturally articulated, it describes a smooth sigmoid curve; this is produced by the shape of the articular surfaces of the centra, and modifications to the neural arches. The anterior portion of the series is convex dorsally. This is achieved by three features : the centra are slightly shorter along their ventral edges than dorsally; the downward inclination of the anterior articular hemispheres; and, by the antero-posterior extent of the zygapophyses, which overhang the centra both in front and behind. Toward

a cup-shaped depression on the ventro-lateral corner of the atlas intercentrum. The shaft, which is elliptical in cross-section, continues without curvature to an unexpanded, blunt and laterally compressed termination. When in position, this rib passes obliquely backwards and downwards from the atlas, beneath the axis and the third cervical centrum.

The *axis rib* is double-headed (fig. 28), as in *Campylosaurus* (GILMORE, 1909), *Ouranosaurus* (TAQUET, 1976) and in fact like most, large ornithopods as

opposed to the smaller hypsilophodontids (*sensu* GALTON) in which it is usually single-headed. This rib is the shortest in the series; its capitulum (c) is blunt and sub-quadrangular, but the remainder of the shaft is compressed and sheet-like. Immediately behind the capitulum, the dorsal edge is developed into a short tubercular process (tu). Posterior to this, the thin dorsal edge descends in a smooth curve to the rounded distal end of the rib, which is slightly curved medially. In articulation, this rib barely extends beyond the posterior margin of the axis centrum.

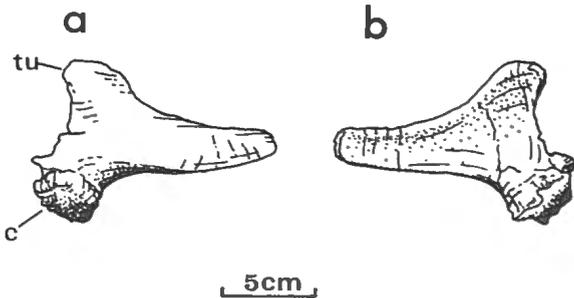


FIG. 28. — *Iguanodon bernissartensis*. (IRSNB. 1561).
Axis rib (left). a : lateral view; b : medial view.

The *third* rib is very similar to, although larger than the axis rib (fig. 29). Its capitulum is supported by a more distinct neck and the shaft of the rib is more rod-shaped distally; the tuberculum is, as in the axis rib, supported on a thin sheet of bone developed from the dorsal edge of the shaft.

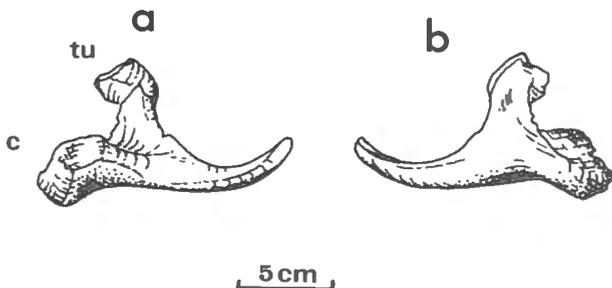


FIG. 29. — *Iguanodon bernissartensis*. (IRSNB. 1561).
3rd Cervical rib (right). a : medial view; b : lateral view.

The *fourth* rib (fig. 30) is perhaps typical of the series. Its two rib heads diverge and are supported on distinct « necks »; these merge distally to produce an elongate rib shaft, which is convex externally and concave internally. Along the dorso-external edge of the capitular process, there is found a small ridge, which in later members of the series becomes a prominent rib-spine (sp - figs. 30, 31, 32). In the succeeding series of ribs, cervicals 5-9, the rib-spine becomes at first more prominent, but gradually diminishes until,

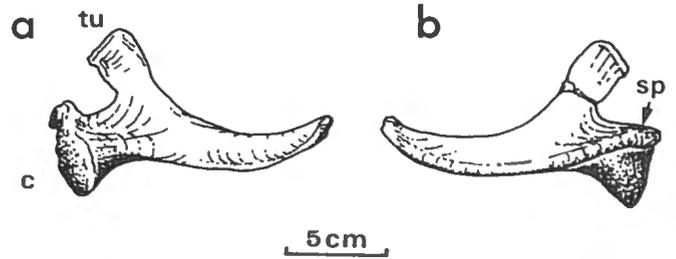


FIG. 30. — *Iguanodon bernissartensis*. (IRSNB. 1536).
4th Cervical rib (right). a : medial view; b : lateral view.

by the ninth, it is once again a low ridge, seen along the outer edge of the shaft on the tenth (fig. 33, ri).

Throughout the series (3-11) the ribs become progressively longer, larger and toward the end of the series, change their orientation. Instead of the main shaft of the rib being directed postero-ventrally, curving gently backwards and downwards from the centrum, it comes to hang almost vertically from the centrum as

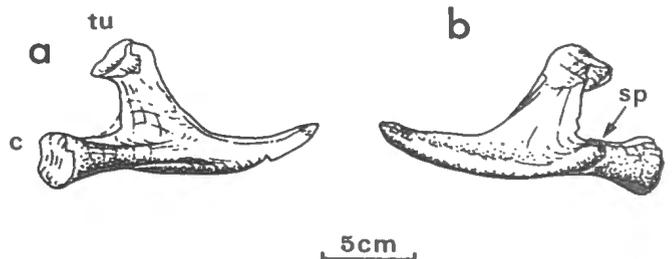


FIG. 31. — *Iguanodon bernissartensis*. (IRSNB. 1536).
5th Cervical rib (right). a : medial view; b : lateral view.

it does in succeeding dorsals. The rib-head structure is therefore modified accordingly: the capitulum remains large and develops a large, long neck, while the tuberculum, although still large, is supported by a much shorter process, similar to the « shoulder » found on the ribs of dorsal vertebrae. These two rib heads also lie in the same transverse plane along the shaft of the rib, rather than diverging at different angles as in early cervicals. By these changes the posterior cervical ribs appear better adapted to support a larger and consequently heavier shaft.

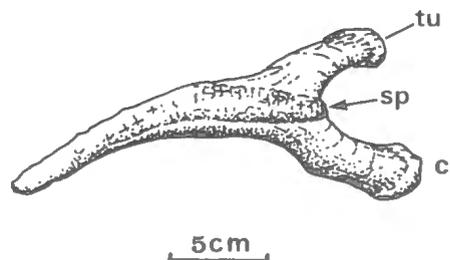


FIG. 32. — *Iguanodon bernissartensis*. (IRSNB. 1536).
8th Cervical rib (right) lateral view.

Dorsal Vertebrae.

There are seventeen dorsal vertebrae, sixteen of which freely articulate with each other; the last, however, is functionally incorporated into the sacrum and, even though it possesses a normal, free dorsal rib, it will be described with the sacrum.

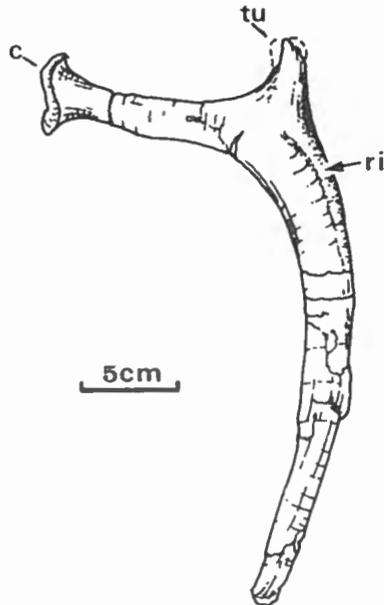


FIG. 33. — *Iguanodon bernissartensis*. (IRSNB. 1536).
10th Cervical rib (left) lateral view.

The dorsal vertebrae which immediately follow the cervical series (figs. 34, 35) demonstrate a gradual diminution of persistent cervical characters. The *first dorsal* (dor. 1) is recognised as the first presacral vertebra to bear a parapophysis (pa) above the neurocentral suture (nc.s - fig. 34). As with the cervicals,

its centrum is quite markedly opisthocoelous and its anterior articular surface is convex. The ventral half of the centrum is quite strongly laterally compressed, thereby producing a large rounded ventral keel, above which the lateral surface is depressed (fig. 35 B). Above the neurocentral suture, the parapophysis is a large vertical depression; it is situated in a V-shaped cleft formed by buttresses of bone which arise from the anterior and posterior corners of the base of each neuropophysis; these buttresses merge dorsally, above the parapophysis, to form a thick buttress which supports the transverse process from beneath. The articular surface for the capitulum of the rib is confined to the posterior surface of the anterior neuropophyseal buttress; its surface is vertically oval and slightly depressed. The neuropophyses are quite short antero-posteriorly compared with later members in this series; they are also quite broad transversely — largely a result of the buttressing for the parapophyses and transverse processes; they also enclose a large, broad neural canal (fig. 36 b). The transverse process is large and arches upwards and outwards, ending abruptly at a blunt, rounded diapophysis. The prezygapophyses are borne on the dorsal surface of each transverse process, at some distance from the mid-line (fig. 35 A) after the fashion of the posterior cervicals. The neural spine arises from the antero-median roof of the neural arch, between the bases of the transverse processes; it arches upward and backward, ending at a slightly hook-shaped apex, from which it descends in a smooth concave curve and divides into two buttresses each of which supports the large divergent postzygapophyses.

The centrum of the *second dorsal* vertebra is also opisthocoelous and has a convex anterior articular surface (fig. 36 a), although these features are some-

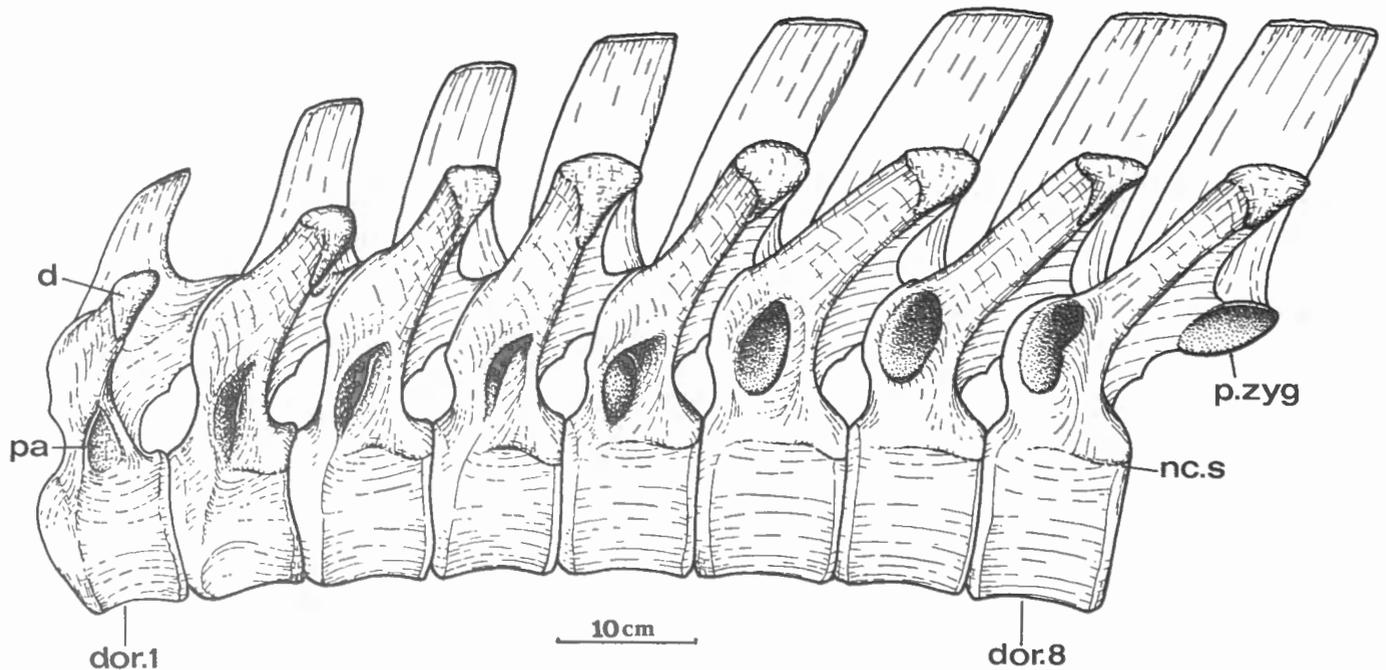


FIG. 34. — *Iguanodon bernissartensis*. Reconstruction of the anterior dorsal vertebral column.
Based on « individu S » of the conservatoire, I.R.Sc.N.B. Lateral view.

what less strongly developed than in the first dorsal. The ventral half of the centrum is less strongly laterally compressed than the preceding, nevertheless, there is still a marked ventral keel; similarly, the sides of the centrum are less depressed (fig. 35 B). The parapophysis has a similar form to that of the first dorsal, although it is positioned slightly higher up on the side of the neural arch. The neural arch is similar in construction to that of the first, but the neural spine is taller and less hook-shaped (fig. 34), the prezygapophyses are closer to the mid-line and the postzygapophyses are somewhat smaller and also closer together.

The *third* and *fourth* dorsal vertebrae continue the change from cervical to dorsal characters. The centrum becomes progressively taller and narrower (figs. 34, 35 B) with a narrower, rounded ventral keel joining the now amphiplatyan (slightly opisthocelous) articular faces. The margin of the articular faces bear quite noticeably everted rims. The sides of the centra are concave longitudinally, convex vertically and merge above with the robust neurapophyses. The parapophyses are similar in shape to those of the preceding dorsals, but are positioned slightly higher on the side of the neurapophysis. Immediately above and medial to the parapophyses are the prezygapophyses, which very slightly overhang the anterior margin of the centrum. Between the adjacent, dorso-medially facing prezygapophyses there is a shallow cleft, ending posteriorly at the anterior edge of the roof to the neural canal; from this roof, there arises the leading edge of

the neural spine. The latter rises steeply before ending at a thickened, truncated dorsal edge. The posterior edge of the neural spine is thin and sharp, as with the anterior edge and, as it descends, it produces on either side a buttress (fig. 39 a) both of which expand to support the postzygapophyses; these are separated by a concave recess. In lateral view, each neural spine is slightly inclined backward, roughly rectangular having the form of a deep but thin blade, and between one-and-a-half and two-times the height of the centrum.

From the antero-lateral edge of each postzygapophysis, there is a thin shelf of bone, which curves forward and outward to the distal end of the transverse process. The latter is elongate and rises obliquely from the side of the neural arch; in cross-section, it is more or less triangular, with a flat or slightly convex dorsal surface, supported ventrally by a thick buttress on either side of the parapophysis. The antero-ventral surface of this buttress bears scars which probably represent the area of attachment for ligaments from the neck region of the rib (between capitulum and tuberculum). The neural canal is small, sub-circular and entirely enclosed by the neurapophyses, which are fused medially, above the neurocentral suture (figs. 36 d, 39 a).

The following series of vertebrae, from dorsal 5 to dorsal 11 (figs. 34, 35, 37, 38) are, apart from relatively minor details, similar in structure. Their centra are extremely narrow and tall, with a narrow ventral keel and everted articular margins. The parapophysis

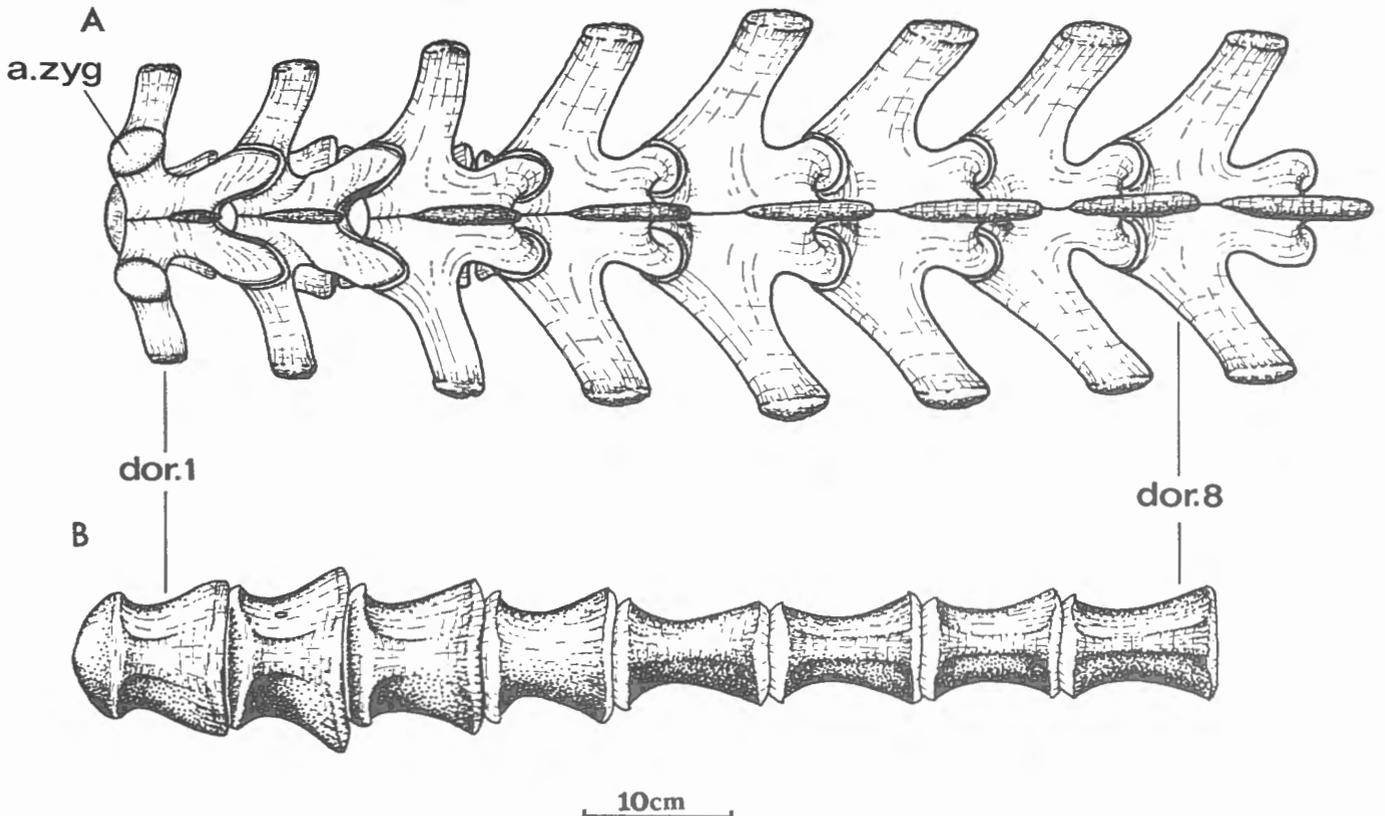


FIG. 35. — *Iguanodon bernissartensis*. Reconstruction of the anterior dorsal vertebral column as in fig. 34. A: dorsal view; B: ventral view.

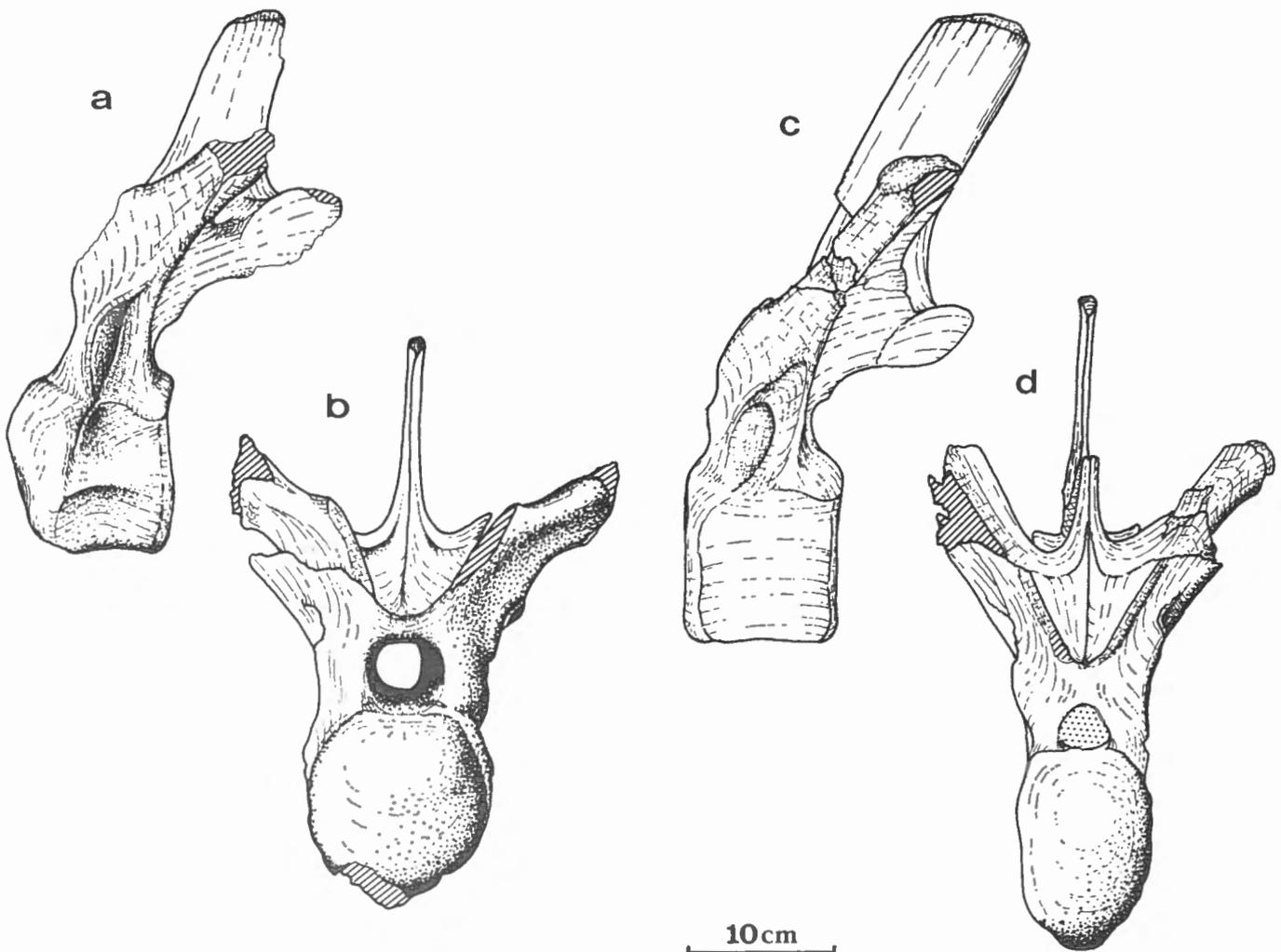


FIG. 36. — *Iguanodon bernissartensis*. (« Individu S ») a, b : 2nd Dorsal vertebra in lateral and anterior views; c, d : 5th Dorsal vertebra in lateral and anterior views.

becomes particularly prominent and in the anterior members of this series, rather rugose in appearance (IRSNB. 1534, fig. 40, ru. par) indicating that the rib-head (capitulum) was probably anchored to the parapophysis by ligaments, instead of having a freely mobile synovial joint. This adaptation no doubt reflects the need to anchor the very large ribs, that these vertebrae carried, securely against the vertebrae.

The posterior members of the dorsal series (12-16) are more antero-posteriorly compressed than are the earlier dorsals. The centra are moderately opisthocelous (fig. 39 d) while their anterior surfaces are flat or very slightly convex; the articular margins are strongly everted, and the centra are noticeably broader than in the anterior dorsals and possess narrow ridge-like ventral keels (fig. 38 B). The centra of the last few dorsals show a slight backward inclination (fig. 37) as if to curve upwards slightly to meet the sacrum posteriorly; in association with this feature, the ventral edge of the anterior articular surface is developed into a slight lip, which underlaps the posterior margin of the preceding dorsal. These slight modifications are pre-

sumably associated with the stresses occurring at the base of the spine when the vertebral column is held in an oblique or horizontal position. The neural arches are extremely robust and enclose a proportionately very small neural canal (fig. 39 c, d); the transverse processes are more slender than in the middle dorsals and project more or less horizontally at the level of the prezygapophyses. The latter are very large, convex, horizontal articular surfaces (fig. 39 c).

There are a few progressive changes which occur along the dorsal series, which can be conveniently summarised as follows. At the beginning of the dorsal series, the *transverse processes* are robust, steeply inclined processes, passing upward and backward from the side of the neuropophysis to form a lofty diapophysis. Progressing down the series they become, at first slightly longer and more robust, but later become more slender and decline in height; in the more posterior members they form relatively slender, horizontal processes. In association with these changes, the *parapophyses* change their characters: initially (fig. 36 a)

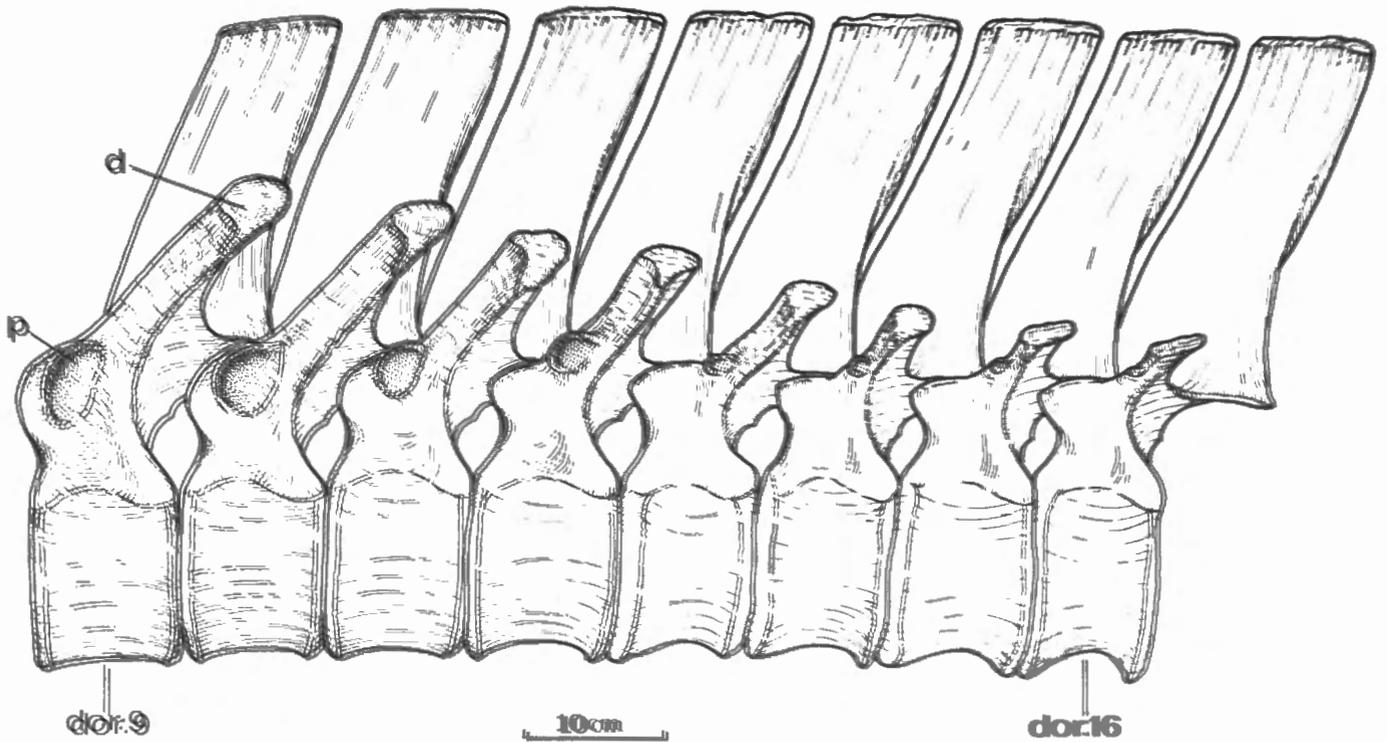


FIG. 37. — *Iguanodon bernissartensis*. Reconstruction of the posterior dorsal vertebral column, based on « Individu S », vertebrae 14 and 16 have been restored. Lateral view.

they are placed low on the side of the neural arch, and verse process and diminish in size. The zygapophyses are of modest size; however, later in the series they become larger, higher and may develop rugose articular pads (figs. 34, 40); farther posteriorly, they rise still

higher and begin to migrate outward along the transverse series: at first they are large, slightly separated and steeply inclined, but later they become closer together and smaller; toward the end of the series they become

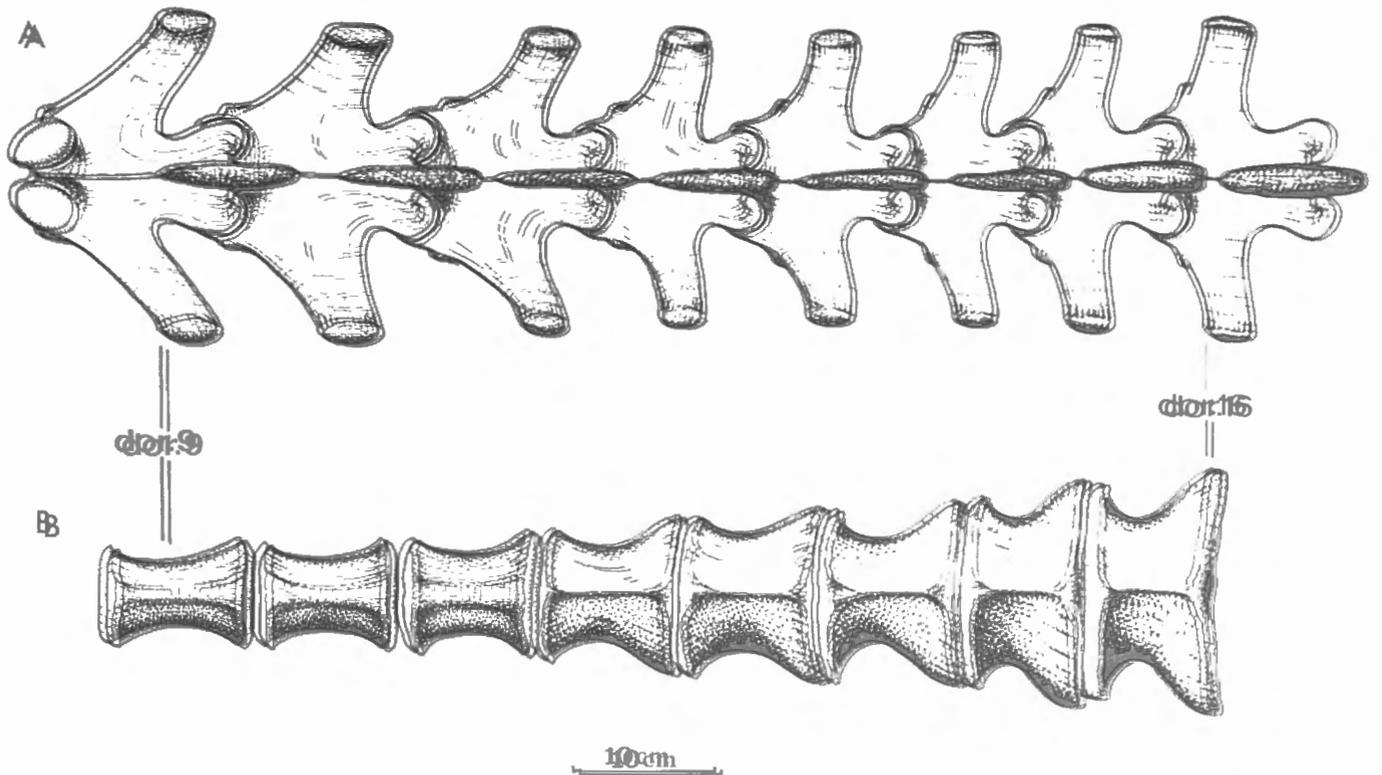


FIG. 38. — *Iguanodon bernissartensis*. Reconstruction of the posterior dorsal vertebral column as in fig. 37. A.: dorsal view; B.: ventral view.

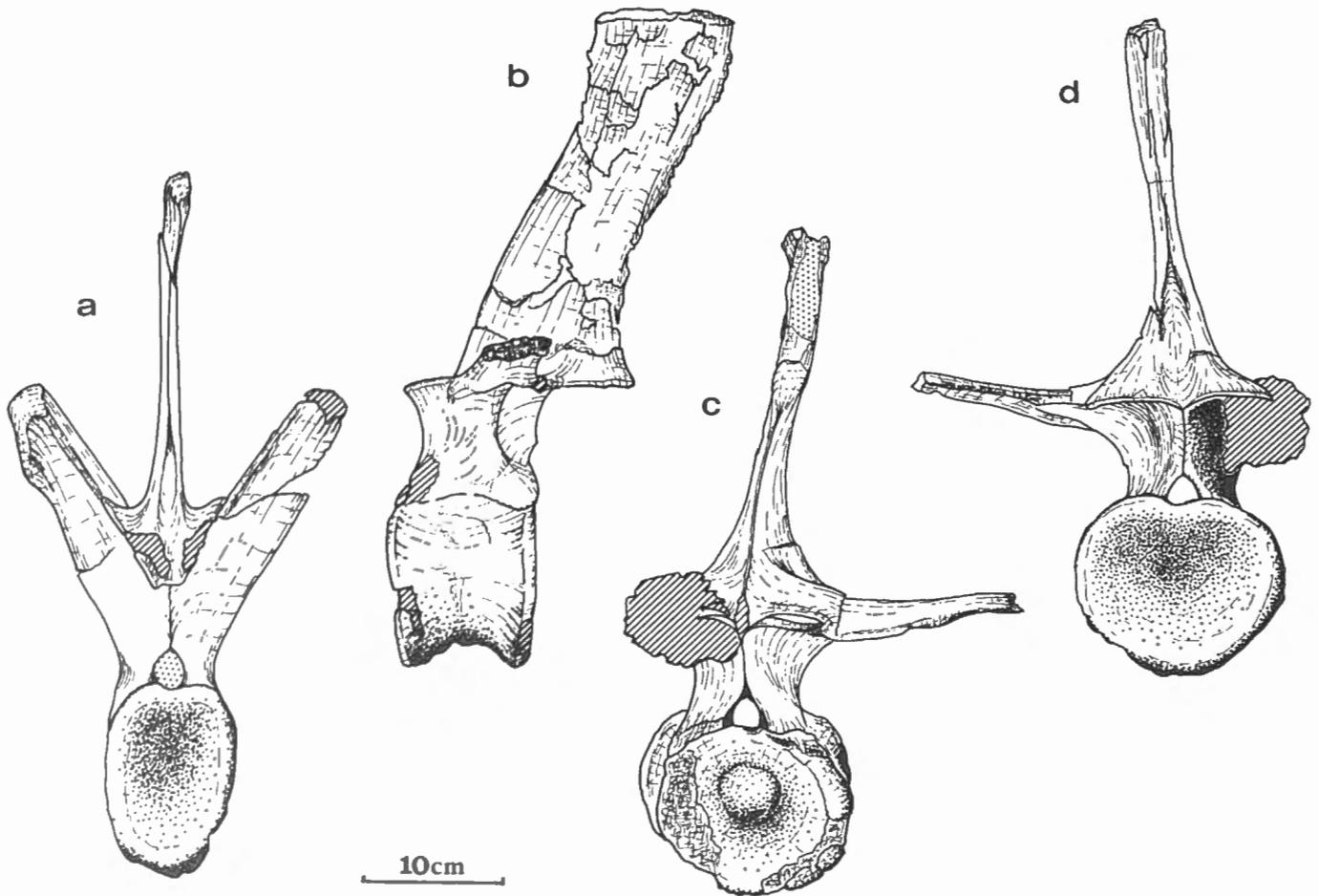


FIG. 39. — *Iguanodon bernissartensis*. (« Individu S »). a : posterior view of 6th Dorsal vertebra; b, c, d : 15th Dorsal vertebra in lateral, anterior and posterior views respectively.

again large and horizontal. As previously alluded to, the *articular surfaces* of the centra are initially strongly opisthocelous with a prominently convex anterior surface; however, both of these features decline so that the middle dorsals are more or less platycoelous, while posterior dorsals become again opisthocelous, but retain an essentially flat anterior surface (with, on occasions, a central notochordal boss - fig. 39 c).

Dorsal Ribs.

The first dorsal rib (fig. 41) although rather larger, is similar in overall shape to the last cervical rib. The capitulum (c) is a small rounded condyle, supported on a long, slender capitular process. The tuberculum (tu) is quite large, has a shallow, depressed articular surface and forms a shoulder region on the rib; beneath the tuberculum the rib shaft curves downward and inward, tapering to a compressed distal tip. In cross-section, the rib shaft is thickened along its external edge.

Successive ribs are progressively larger and longer, reaching a maximum rib shaft length of approximately 110 cms, at dorsal rib 7 or 8. The capitulum becomes correspondingly deeper and is supported by a proportionately shorter and thicker capitular process. The dorsal edge of this process become scarred and pitted

(fig. 42 rug) where connective tissue seems to have bound it to the transverse process of the neural arch against which it lay. This adaptation enabled the neural arch to support the massive anterior dorsal ribs more easily — a few specimens (IRSNB. 1534 - fig. 40) appear to demonstrate that connective tissue also reinforced the parapophyseal facets. The tuberculum forms a small lip on the shoulder of the rib and its articular surface in a shallow depression directed postero-medially. From the antero-dorsal edge of the tuberculum a prominent rounded ridge (fig. 42 ri) curves downward across the anterior surface of the rib shaft and forms a rounded leading edge to the rib farther distally. The series of very large dorsal ribs between positions 3 and 9 have noticeably blunt distal ends to their shafts (fig. 42 bl); these probably indicate that the ribs articulated against cartilaginous sternal ribs.

In more posterior members of the dorsal series, the rib shaft becomes progressively shorter and more slender, and the shoulder region is lost. The capitulum becomes smaller and the tuberculum becomes flap-like, overlapping the distal end of the transverse process (fig. 43 a, b). In the more posterior ribs, the articular heads approach one another and are separated by only a short step (fig. 43 c, d). The seventeenth dorsal

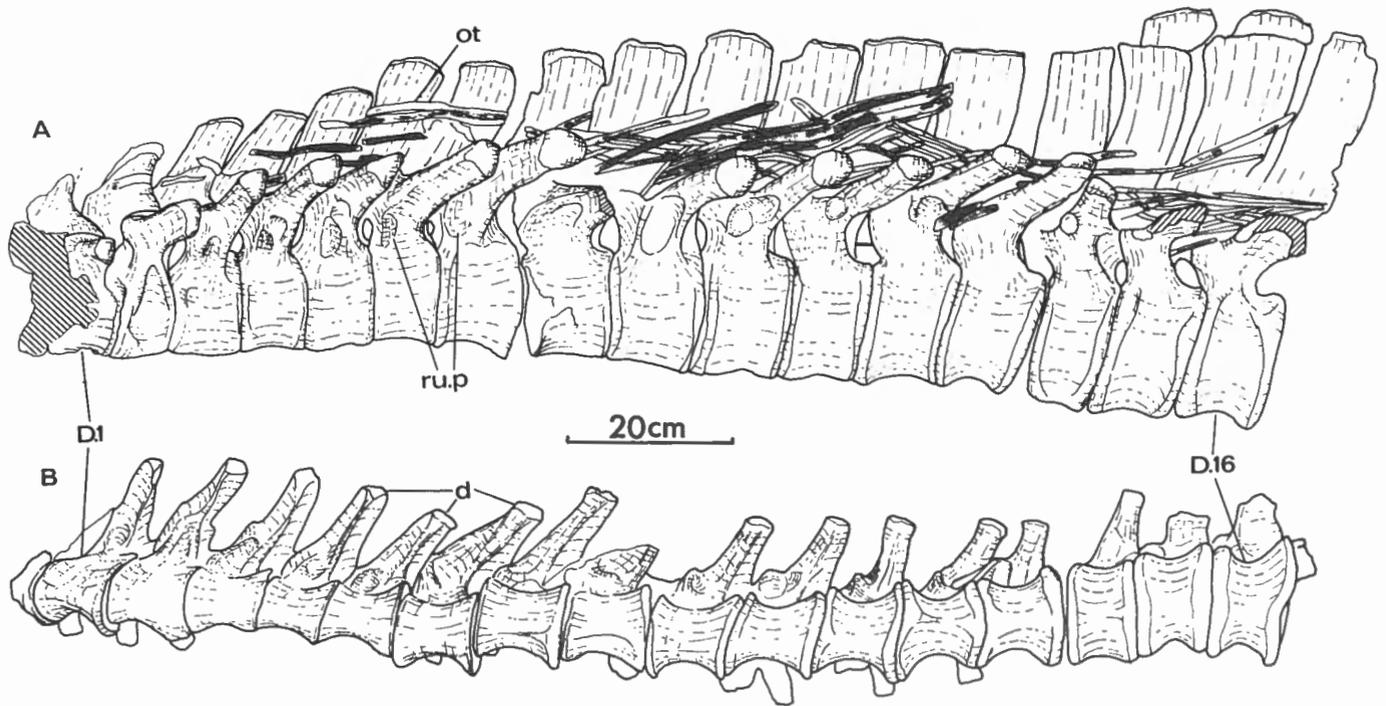


FIG. 40. — *Iguanodon bernissartensis*. (Holotype. IRSNB. 1534). The articulated dorsal vertebral column, as preserved. A: lateral view; B: ventral view.

vertebra possesses a blunt-ended transverse process, which suggests that the last dorsal rib was single-headed, as it is in *I. mantelli*.

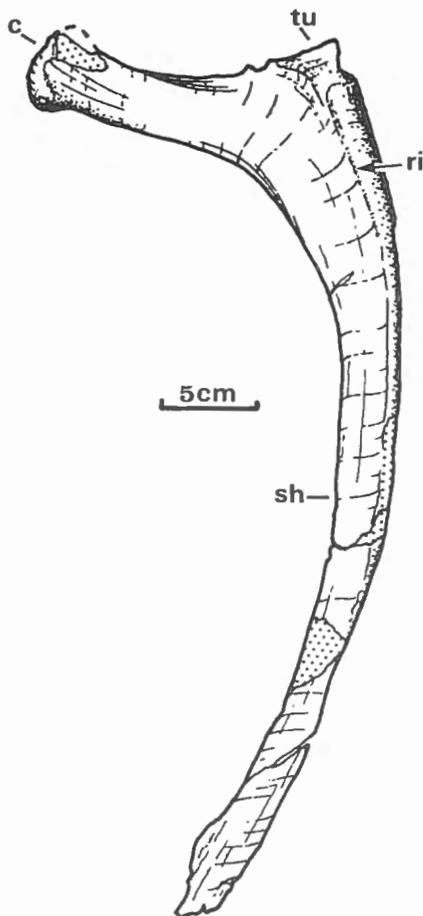


FIG. 41. — *Iguanodon bernissartensis*. (IRSNB. 1536). 1st Dorsal rib (left) in anterior view.

The Sacrum.

The sacrum of *I. bernissartensis* typically comprises eight fused vertebrae, of which seven are true sacrals, insofar as they possess pairs of sacral ribs. The additional vertebra incorporated into the sacrum is presacral in origin. Several specimens from Bernissart possess practically entire sacra. Unfortunately, these specimens have not been as fruitful as would have reasonably been expected, through a combination of poor preservation, lack of preparation, inaccessibility and fragility. Representative examples of the sacrum of this species are illustrated (figs. 44, 45). The general organisation of the sacrum of this species can be summarised as follows.

The first vertebra of the sacrum bears a free dorsal rib and is therefore recognised as a member of the dorsal series which has become fused to the first true sacral. This « sacro-dorsal » vertebra (sd - fig. 44) has a broad sub-rectangular centrum, with a flat or slightly convex anterior articular surface and an everted margin. Behind the articular face, the centrum is contracted and the lateral and ventral sides are rather flattened. Posteriorly, the centrum is again expanded where it meets and is fused to the first true sacral. The lateral sides of the posterior part of the centrum are expanded where they support the first sacral ribs. Dorsally, the neural arch possesses large forward projecting prezygapophyses, behind which the transverse processes curve upward and outward as flattened and abruptly truncated processes (d). The postzygapophyses are fused with the prezygapophyses of the succeeding vertebra. The neural spine is very similar to that of the dorsal vertebrae.

BERNISSARTENSIS FROM THE LOWER CRETACEOUS OF BERNISSART (BELGIUM)

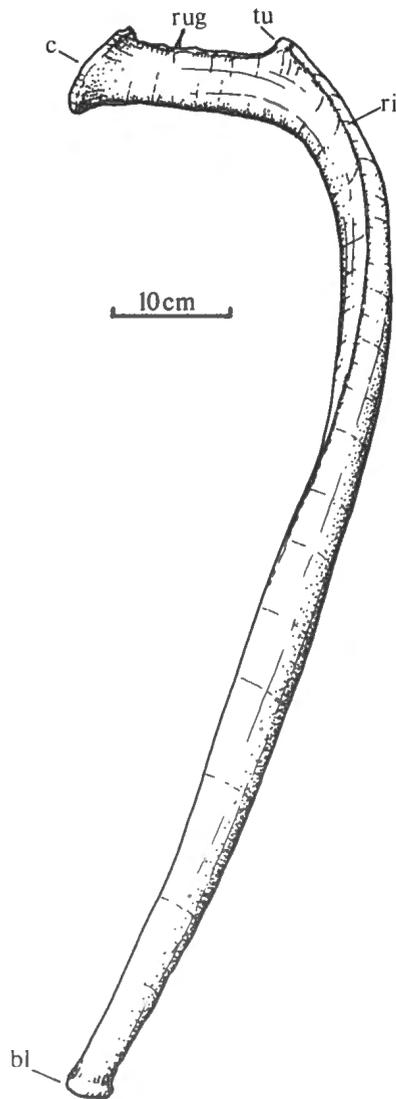


FIG. 42. — *Iguanodon bernissartensis*. A typical anterior dorsal rib, anterior view.

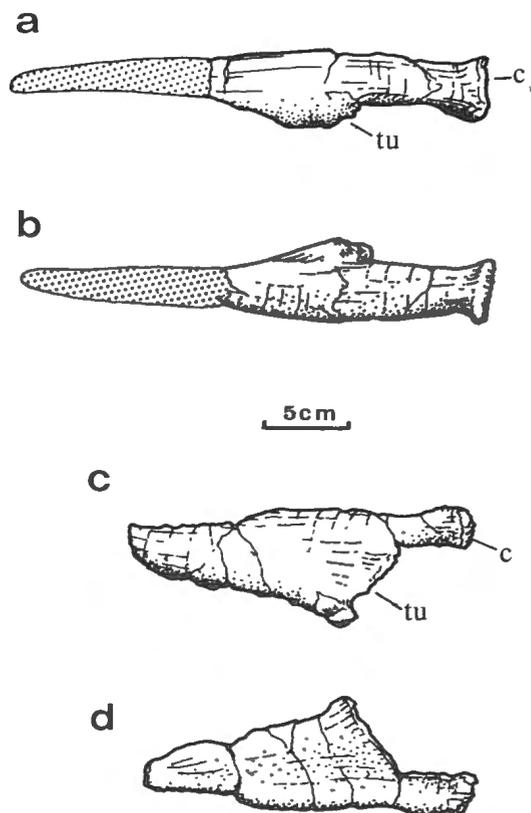


FIG. 43. — *Iguanodon bernissartensis*. (Holotype. IRSNB. 1534). a, b : 14th Dorsal rib in dorsal and ventral view respectively. c, d : 16th Dorsal rib in dorsal and ventral view respectively.

surface is flattened rather than depressed; its posterior articular surface is very broad, slightly depressed (platycoelous) and its margins are everted. Dorsally, the transverse process/sacral rib is positioned over the middle of the centrum as it is in adjacent caudal vertebrae (fig. 45 A, s. 7). In lateral view, the ventral surface of the sacrum describes a smooth scalloped arch and the neural spines are tall and separate.

The centrum of the first true sacral is broadly expanded anteriorly and posteriorly, where it is fused to adjacent centra and also supports the sacral ribs -- its own anteriorly and those of the second sacral posteriorly. Between these ends, the centrum is strongly contracted, the lateral walls being almost vertical and concave antero-posteriorly, with the ventral surface forming a broad rounded keel. The neural arch of this vertebra has shifted forward so that it lies across the hind end of the sacro-dorsal centrum. This forward displacement of the neural arch occurs throughout the sacral series and forces the lateral spinal nerves (n.ca - fig. 44) to exit across the dorsal surfaces of the centra, rather via the intervertebral spaces, as is usual in the presacral and caudal vertebrae.

In succeeding sacrals, the centra, at first narrow and keeled, become progressively broader and more massive, and the ventral surface develops a broad and shallow haemal sulcus (fig. 45, h.s). The last sacral is the largest of the posterior sacrals and its ventral

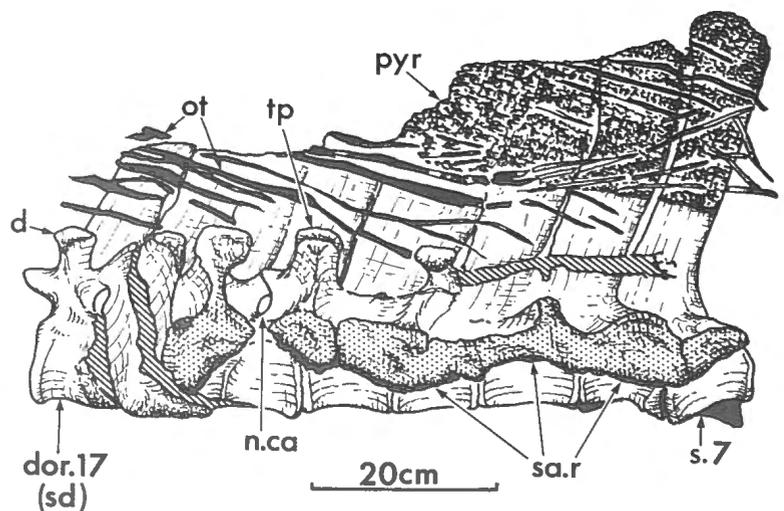


FIG. 44. — *Iguanodon bernissartensis*. (IRSNB. 1729). The Sacrum. Lateral view as preserved. Sacral rib yoke emphasised by even stippling, broken bone cross-hatched.

Each sacral rib (sa. r - fig. 44) is borne at the co-ossified junction between the sacral centra. The base of each rib is firmly fused to the ventral surface of the transverse processes, to the lateral surface of the neural arch pedicels and to the lateral intercentral suture. The first four sacral ribs are particularly robust and their ventral portions are expanded so that they fuse together lateral to the sacral centra to produce a massive bar; this bar or yoke is in turn firmly attached to the medial surface of the ilium above the acetabulum. The more posterior sacral ribs, which also contribute to the sacral yoke, are rather dorso-ventrally compressed; these back on to the medial surface of the post-acetabular portion of the ilium.

sacral yoke which supports the pelvis, it does not appreciably strengthen the sacrum. Most probably, this variation is probably of pathological origin. The long heavy tail of the species was normally held clear of the ground. The enormous compressive stresses involved in supporting the tail would have been concentrated upon the base of the tail particularly at the junction of tail and sacrum. Weakness at this point may have resulted in breakdown of the joint, leading to eventual fusion.

No obvious sacral variation, apart from that referred to above, has so far been noted in *I. bernissartensis*, although considerable variation is known in the related species *I. mantelli* (NORMAN, in prep.).

Caudal Vertebrae.

Several of the specimens from Bernissart possess almost complete articulated tails, which show adequately the main features of this series (fig. 46). In one of the more complete specimens (IRSNB. 1726) the tail, as preserved, comprises forty-six articulated vertebrae. It seems unlikely that there were very many more than this in the tail of *I. bernissartensis*, and fifty would seem to be a reasonable estimate of the maximum number of caudal vertebrae.

The first caudal vertebra (figs. 46, 47) is typically broad, almost square in end view and rather obliquely inclined forward. The articular surfaces of the centrum are broad and platycoelous, although the dorsal half of the anterior surface bears a slight convex swelling which articulates against a corresponding recess in the upper part of the posterior surface of the last sacral centrum. The lateral and ventral sides of the centrum are more or less flat and meet at rounded corners; the margins of the articular faces at each end are thick and everted. Dorsally, the sides of the centrum sweep upward and outward into the base of the caudal rib (transverse process - Ca. r). The caudal rib curves outward horizontally as a dorso-ventrally flattened, wing-like process. Above the caudal rib, the neural arch is low and stands upon extremely robust pedicels. The prezygapophyses project obliquely forward, and between them the large neural spine curves upward

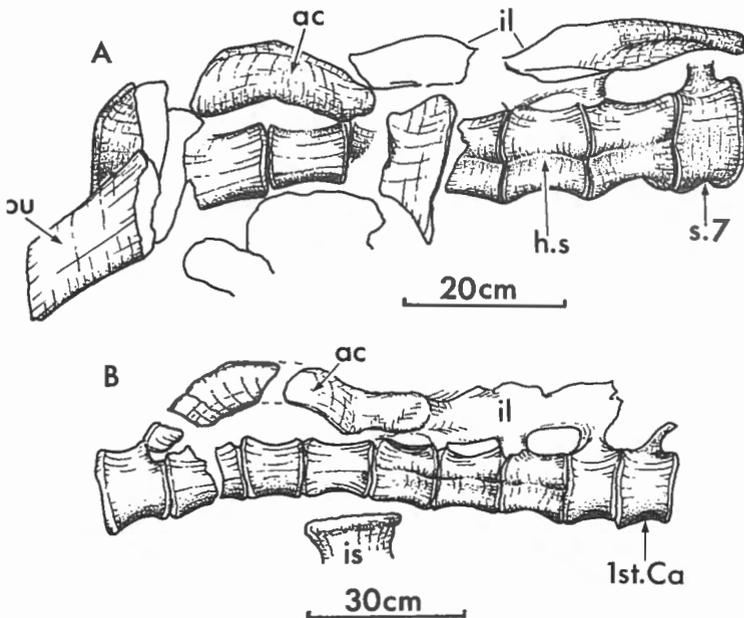


FIG. 45. — *Iguanodon bernissartensis*. The sacrum. A: IRSNB. 1722, as preserved, in ventral view; B: IRSNB. 1535, as preserved, in ventral view.

Sacral Variation. — One of the individuals (IRSNB. 1535 - fig. 45 B) possesses a sacrum composed of nine fused vertebrae, one more than is usual for this species. The precise reasons for the addition of a caudal vertebra to the sacrum are not clear. Since its caudal ribs are entirely free and are not fused to the

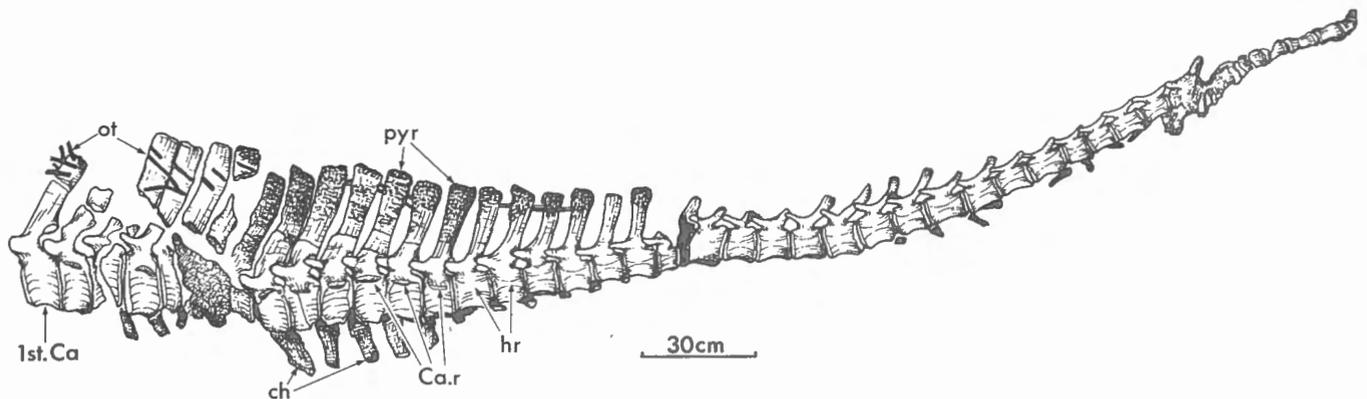


FIG. 46. — *Iguanodon bernissartensis*. (IRSNB. 1729). The articulated tail vertebrae, as preserved « en gisement ».

and backward to a blunt, thickened, dorsal edge. The posterior edge of the neural spine bears, near its base, the postzygapophyses (p. zyg) which are directed ventrolaterally. The postero-ventral margin of the articular surface of this vertebra does not seem to have borne a haemal arch (chevron bone) and consequently does not bear the everted edged haemapophysis found in later caudals.

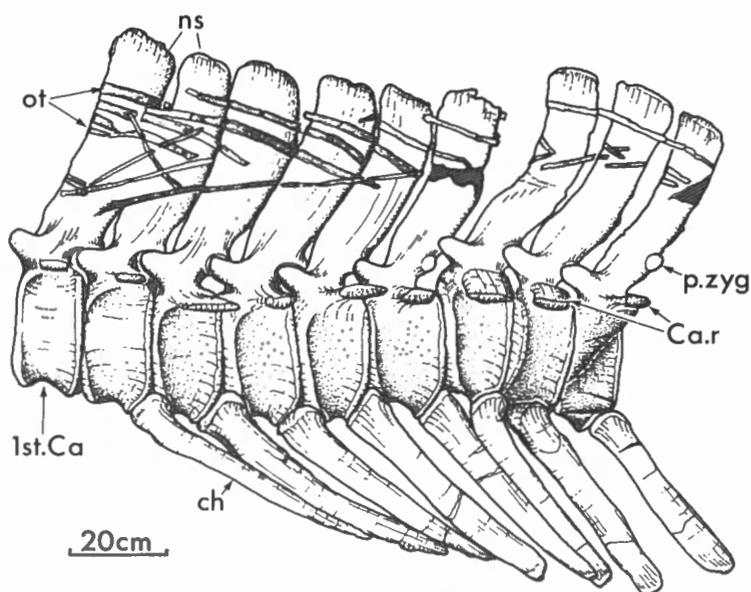


FIG. 47. — *Iguanodon bernissartensis*. (Holotype. IRSNB. 1534). Articulated series of anterior caudal vertebrae (1-9). Even stippling indicates « carton pierre » restoration.

The second caudal vertebra is slightly less broad than the first, its articular surfaces having a more rectangular appearance in end view. Ventrally, the body of the centrum is rather narrow and forms a short, thick, rounded keel. The centrum is also rather tilted forward, as in the first caudal. The tilting of the anterior members of the caudal series produces a slight, but distinctive, slope to the base of the tail as it drops away from the sacrum — a similar phenomenon was also noted in the posterior dorsal vertebrae. The lateral sides of the centrum are approximately flat between the everted margins. The remaining characters of caudal rib, neural arch and neural spine are similar to those of the first caudal vertebra. The postero-ventral margin of the centrum bears the first haemapophysis, which allows articulation of the anterior half of the head of the haemal arch (fig. 47, ch). The articular surface consists of a moderately deep excavation in the ventral edge of the centrum, around which there is a thickened lip of bone.

In succeeding anterior caudal vertebrae (3-14) the vertebral form remains more or less constant (figs. 46, 47). All are quite strongly laterally compressed, with flattened sides and rounded keels to the centra; their articular faces are platycoelous and roughly rectangular in end view. The ventral margins of both articular

faces bear large haemapophyses; the posterior one is always the more prominent of the two. The caudal ribs, which are large and flattened anteriorly, become progressively shorter along the series; they also bear prominent surface striae, which probably represent areas for attachment of part of the caudi-femoral musculature. The most notable changes in form of the caudal vertebrae toward the end of this anterior series are: a gradual decrease in overall size, a decrease in height of the neural spine and a reduction in size of the caudal rib. At about the fourteenth caudal, the caudal rib is reduced to a small nubbin prior to being altogether lost. This transition is used as a marker for the change from the anterior to middle caudal series.

The middle caudal vertebrae (figs. 46, 48) steadily decrease in size posteriorly from caudal fifteen to the late thirties; the last of the series is the last to bear a haemal arch. The centra of the anterior members of

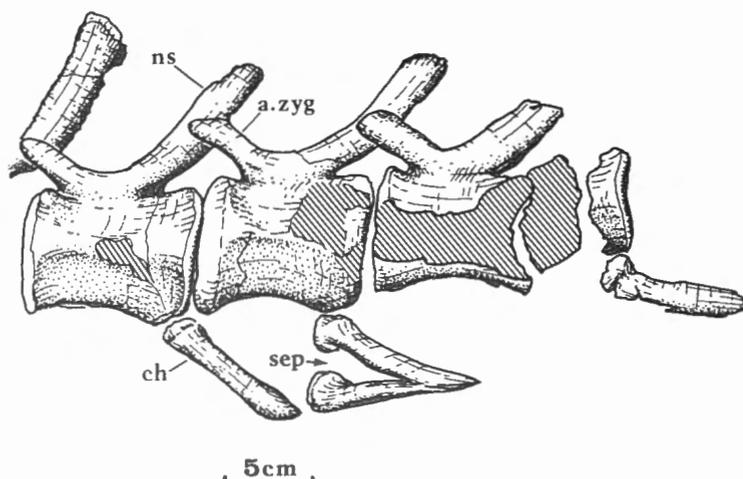


FIG. 48. — *Iguanodon bernissartensis*. (IRSNB. 1725). Posterior caudal vertebrae, as preserved « en gisement ». Cross-hatching represents broken surfaces.

this series are rather taller than broad, hexagonal cylinders, with platycoelous articular faces. A horizontal ridge (hr, fig. 46) on the side of the centrum is all that remains of the caudal rib. The angular sides of the centrum become more accentuated along the series. Between the haemapophyses, the ventral surface is flat. The neural arch is low and narrow and carries the tall, backwardly inclined neural spine. The prezygapophyses are prominent, oblique and clamp around postzygapophyses which are perched on the postero-lateral sides of the neural spine. Toward the end of the middle caudal series, the neural spines become shorter and eventually become short apophyses which support the post-zygapophyses. Similarly, the chevrons become smaller and the proximal end becomes divided into separate heads (fig. 48).

The remainder of the tail consists of eight to ten posterior caudals. These have small, narrow, cylindrical centra (fig. 49) upon which are perched very abbreviated neural arches. The latter consist of small

arches, forming a loop of bone over the neural canal, from which project the zygapophyses.

It is not uncommon to find two caudal vertebrae fused together; this is undoubtedly a pathological condition resulting from injury to the tail during the life of the dinosaur.

the first: the haemal spine is larger and more blade-like than style-like (figs. 47, 50). Farther back along the tail, the chevrons steadily decrease in size, paralleling the decline in height of the neural spines. The haemal arches disappear altogether by about caudal 40 and the last members of the series have the proximal end

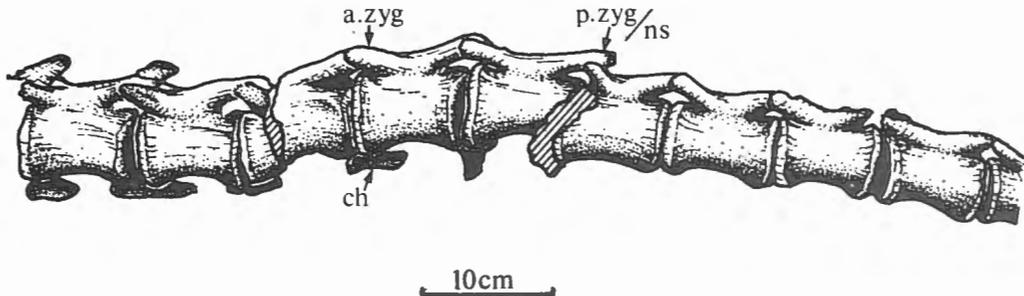


FIG. 49. — *Iguanodon bernissartensis*. (IRSNB. 1715). Posterior caudal vertebrae, as preserved « Monté ».

Haemal Arches (Chevron bones).

The first haemal arch articulates between the second and third caudal vertebrae (fig. 47 - IRSNB. 1534). The proximal (articular) end of this chevron is expanded and divided by a transverse ridge into anterior and posterior facets which articulate against the haemaphyses of adjacent vertebrae. Below the head, there is a large neural canal; beneath this canal, the haemal arches coalesce to form a transversely compressed haemal spine (fig. 47) which is curved backward and tapers to a pointed distal end.

separated into two distinct articular heads, which appear to contact the posterior haemaphyses alone (fig. 49).

Ossified Tendons.

The ossified tendons are quite well-preserved and relatively little disturbed in a number of specimens from Bernissart. Ossified tendons are found throughout most of the length of the vertebral column from cervical vertebra 10 backward to about caudal 20. They are found, scattered more or less regularly on either side of the neural spines, on the transverse processes of dorsal vertebrae, on the sacral ribs and occasionally on the lateral surface of the centra of the middle caudal series (IRSNB. 1716).

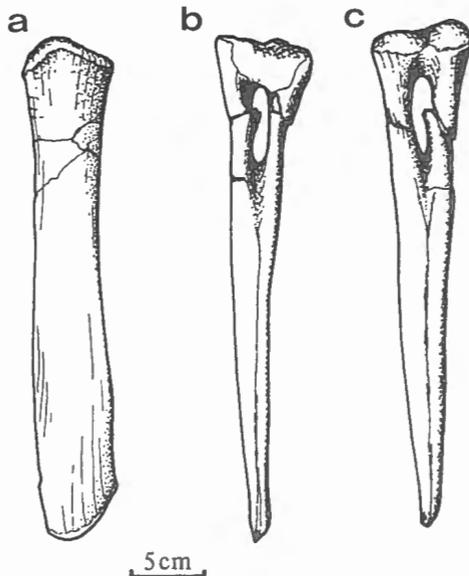


FIG. 50. — *Iguanodon bernissartensis*. (IRSNB. 1561). Chevron bone (haemal arch) as preserved. a: left lateral view; b: anterior views; c: posterior view.

The following six to eight haemal arches are the largest of the tail and differ in shape but slightly from

The external surface of these tendons is longitudinally striated, and they tend to show considerable variation in form: many are long (50 cms and more) thin, bony rods, which may be thin and flattened, rounded, elliptical or angular in cross-sectional view. They do not appear to have been fused either to the neural spines or the transverse processes of vertebrae, since no scars which might be attributable to ossified tendons can be seen on the surfaces of these structures. In addition, the ossified tendons are found to be displaced and sometimes lost in otherwise undisturbed and fully articulated carcasses.

Anteriorly, the first ossified tendons (ot - figs. 40, 41) pass backward and downward from the upper part of a neural spine across the neural spines of the posterior cervical and anterior dorsal vertebrae, terminate (presumably) at the base of a neural spine (fig. 40 - IRSNB. 1534). In one specimen (IRSNB. 1726) a single, rather broad, flattened ossified tendon seems to divide into several subsidiary long tendons which spread outward and backward across successive neural spines. Similar, though much smaller tendons have

been described by GALTON (1974) in the ornithopod *Hypsilophodon*; however, these were only found in clusters around the distal end of the tail.

The typical middle-posterior dorsal arrangement of ossified tendons was described by DOLLO (1887). It consists of a roughly rhomboidal lattice of tendons comprising a deep layer of tendons which run downward and backward across the neural spines, and a more superficial layer running backward and upward across the former layer (figs. 40, 51). DOLLO referred to the lattice as « ligaments ossifiés » which he regarded as being derived from the *M. sacro-lumbalis* complex, described in *Apteryx* by OWEN (1842). DOLLO (*op. cit.*) drew attention to the presence of several fragmented ossified tendons perched along the top of the neural spines in IRSNB. 1561 (fig. 51). He suggested that these were ossified remnants of the *ligamentum apicum dorsalis*; these tendons are in fact broken remnants from the tendon lattice which were presumably displaced during fossilisation. This argument also applies to tendons found on the transverse processes: the *ligamentum transversaria* of DOLLO.

Posteriorly, the lattice arrangement of tendons

surface of the middle caudal centra (IRSNB. 1716); these are, however, probably displaced tendons.

The overall arrangement of ossified tendons is as follows: they are relatively few in number anteriorly, becoming progressively more numerous over the posterior dorsal, sacral and anterior caudal regions, where they are arranged in a two-layered lattice; they rapidly dwindle in number and disappear in the middle caudal region. Apart from the sacral region, the ossified tendons do not appear to have any firm sutural attachment to the underlying neural spines. Therefore it seems probable that, outside the sacral region, the ossified tendons were anchored to the vertebral column by either connective tissue or muscular tissue. Dorsally, the tendons of both deep and superficial layers inserted along the apical region of the neural spines, perhaps attached on either side to an aponeurosis above the apices of the neural spines. (Such an insertion seems logical from a mechanical point of view and also helps to explain the thick, rugose dorsal edge to the neural spines). The area of insertion for the ventral ends of the ossified tendons is similarly problematical. Potentially there are several places for insertion: the

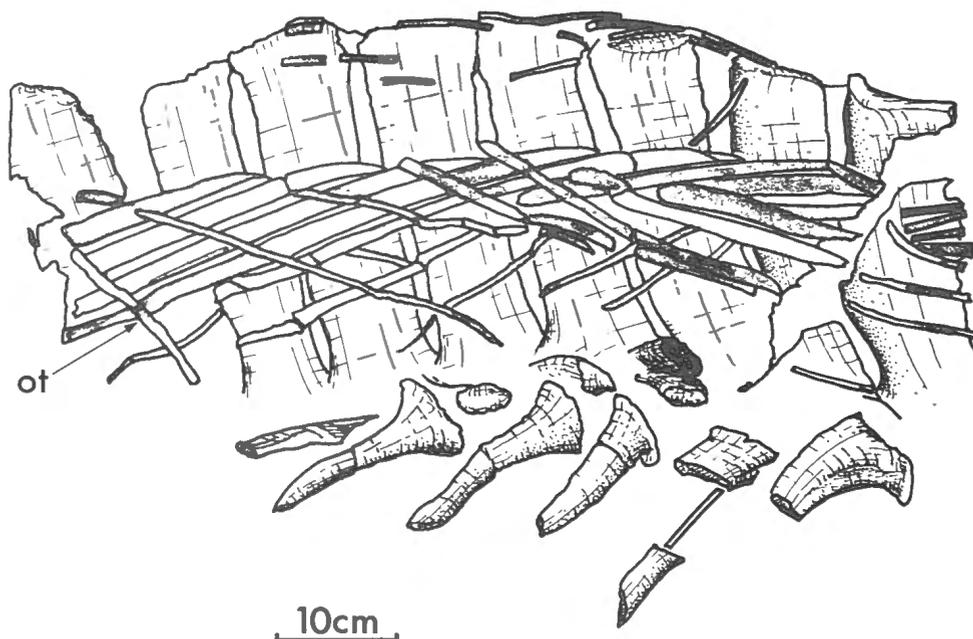


FIG. 51. — *Iguanodon bernissartensis*. (IRSNB. 1561). Ossified tendons as preserved on the neural spines of the posterior dorsal vertebrae. Right lateral view.

crosses the sacrum and continues along the caudal series (fig. 47). In *I. mantelli* (IRSNB. 1551) it can clearly be seen that many ossified tendons fuse to the sides of the sacral neural spines. It seems reasonable to suppose that this also occurred in *I. bernissartensis*, but none of the specimens of this species provide conclusive evidence. Progressing along the tail, the number of ossified tendons decreases and are usually absent beyond the twentieth caudal vertebra. A few tendons have been observed lying along the lateral

base of the neural arch, the transverse processes or the proximal ends of the ribs. At the moment there is little evidence to suggest which of the above is more probable.

Ossified tendons most probably derive from parts of the epaxial musculature. The transformation from muscle tissue into ossified rods was, most probably, a metabolic economy. The normal posture of these animals was one in which the vertebral column was held more or less horizontally: pivoted at the tips.

The constant tendency of the vertebral column to sag, as a result of gravity, required a constant tensile resistance from the epaxial musculature; the metabolic drain created by this postural stress was greatly relieved by the substitution of bony, tensile rods for the epaxial musculature. A more detailed analysis of the structure and function of ornithischian ossified tendons is in preparation.

THE PECTORAL GIRDLE AND FORELIMB.

The *scapula* (fig. 52) is stoutly constructed by comparison to that in most ornithopods; it is also somewhat bowed, so that it follows the contour of the rib cage

glenoid (gl); the distal portion or scapular blade forms a thick, relatively little expanded blade, the top of which is bluntly truncated, rugose and may have been capped by a supra-scapular cartilage. Slightly above the anterior part of the coracoid suture, the edge of the scapula is developed into a thickened boss (b) the « clavicle facet » of others. A thick buttressing ridge (an incipient scapular spine) passes backward from this boss and curves upward to merge with the scapular blade. Behind the scapular spine, the external surface of the scapula is depressed, but swings outward near the posterior edge, where it forms a massive, twisted and hook-shaped buttress of bone, above the glenoid (fig. 52 B). The glenoid forms a large crescent-shaped concave depression (fig. 52 B, gl); the ventral edge of this articular surface is sutured to the coracoid, which forms the lower half of the glenoid. The coracoid suture (cor. s) is extremely rugose and broad. The internal surface of the scapula, along the coracoid suture, bears a shallow groove which forms a portion of an internal passage continuing from the coracoid foramen (fig. 52 C, gr).

The thick, rugose dorsal edge of the *coracoid* is sutured to the scapula (fig. 53, s.s); at the posterior end of this suture, there is an oblique concave depression: the lower half of the glenoid (fig. 53 B, gl). Beneath the thickened margins of the glenoid, the posterior edge of the coracoid is embayed and meets the lower border of the coracoid at a blunt, hook-like process. The lower edge of the coracoid is thickened, rugose and curves forward and upward, eventually meeting the scapular suture. The anterior portion of this edge is notably thickened by a raised ridge on the external surface of the coracoid (fig. 53 D, ru); as will be seen later, this edge probably articulated against an ossification in the sternal cartilage. Apart from the prominent ridge anteriorly, the convex external surface of the coracoid is marked by a large muscle scar (sc) (*M. costo-coracoideus*) near the posterior edge, and also by a notch-shaped coracoid foramen (c. for) along the posterior portion of the scapular suture (fig. 53 A).

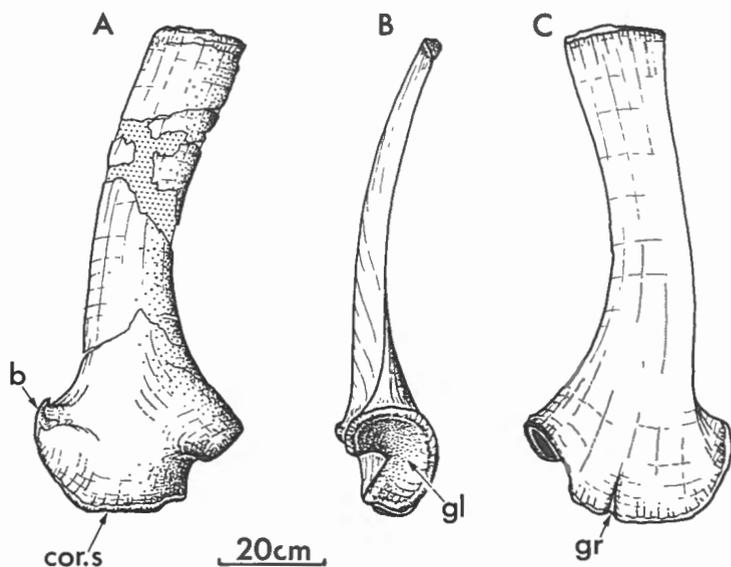


FIG. 52. — *Iguanodon bernissartensis*. Scapula (left).
 A : lateral view (Holotype. IRSNB. 1534) as preserved;
 B : posterior view (restored); C : medial view (restored).
 Even stippling represents areas restored with « carton pierre ».

against which it lies (fig. 52 b). The proximal end is broad and expanded, where it is sutured to the coracoid and bears posteriorly, the dorsal part of the

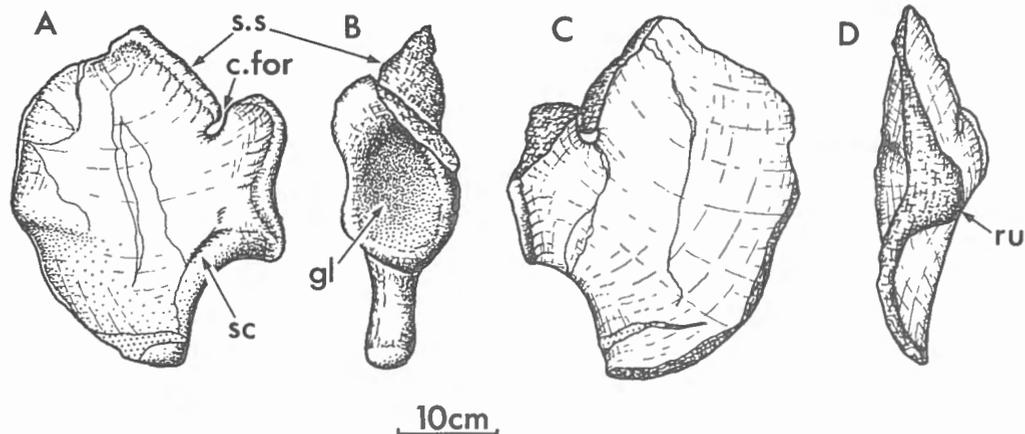


FIG. 53. — *Iguanodon bernissartensis*. (Holotype. IRSNB. 1534). Coracoid (left).
 A : lateral view; B : posterior view; C : medial view; D : anterior view.

BERNISSARTENSIS FROM THE LOWER CRETACEOUS OF BERNISSART (BELGIUM)

The paired *sternal bones* lie either side of the midline, immediately behind the coracoids. Each sternal bone is rather hatched-shaped (figs. 54, 56, st).

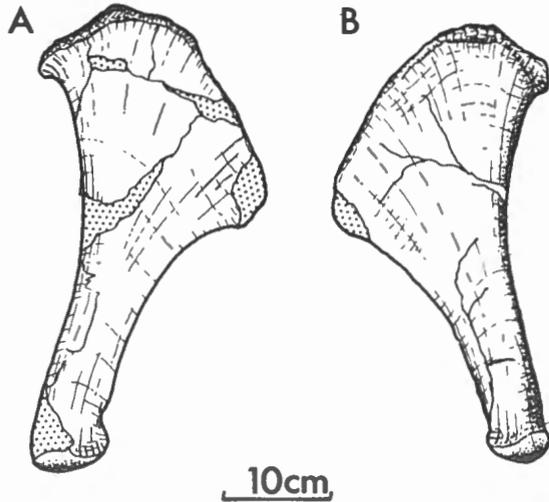


FIG. 54. — *Iguanodon bernissartensis*. (Holotype. IRSNB. 1534). Sternal bone (left). A : internal view; B : external view. Even stippling represents areas restored with « carton pierre ».

The external surface of the « blade » is flat and its medial edge is thin, rugose and slightly curved. Farther anteriorly, this edge becomes thicker and curves outward. From the blunt, rounded anterior extremity, the lateral surface of the sternal bone curves backward and outward to produce an elongate posterior process, which ends at a blunt, slightly everted end — most probably, this blunt end formed the focal point for attachment of some cartilaginous sternal ribs. The median edge of this sternal process curves forward and

inward to meet the postero-medial corner of the « blade ».

The sternal bones appear to have been slightly separated along the midline by a thin strip of sternal cartilage, which broadens anteriorly to link with the coracoids. These bones have in many instances been preserved *in situ* (fig. 55).

An unusual, irregular bony structure has been found in most of the individuals of *I. bernissartensis*. This structure was mentioned very briefly by DOLLO (1882 a), but it has since remained unstudied. It is present, *in situ*, in several of the *en gisement* specimens (fig. 55, int. st) and has been faithfully reconstructed in the correct position in several of the mounted specimens (fig. 56). It is always found in the area between the anterior ends of the sternal bones and between the coracoids; its shape is irregular and its surface is of a rough texture, but there is usually a groove found along its lateral edges which seems to correspond with the adjacent, free edges of the coracoids.

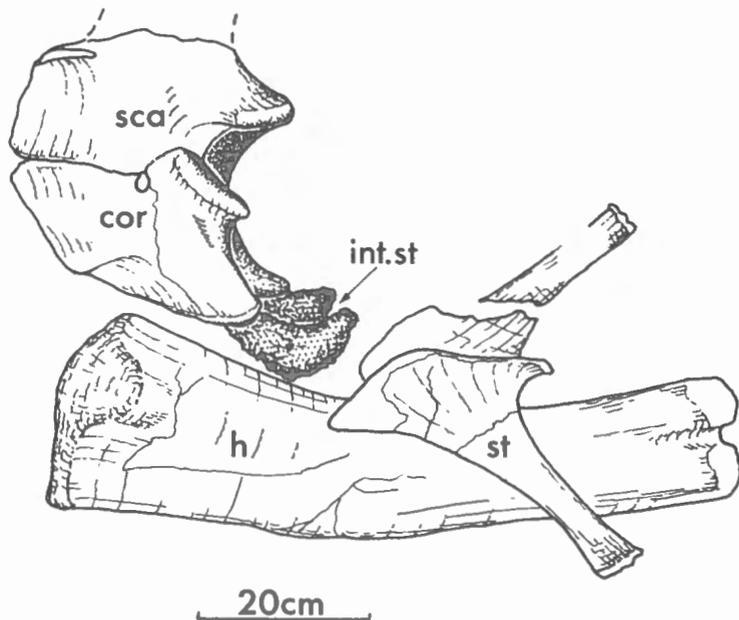


FIG. 55. — *Iguanodon bernissartensis*. (IRSNB. 1535). Sternal region of an articulated skeleton « en gisement ».

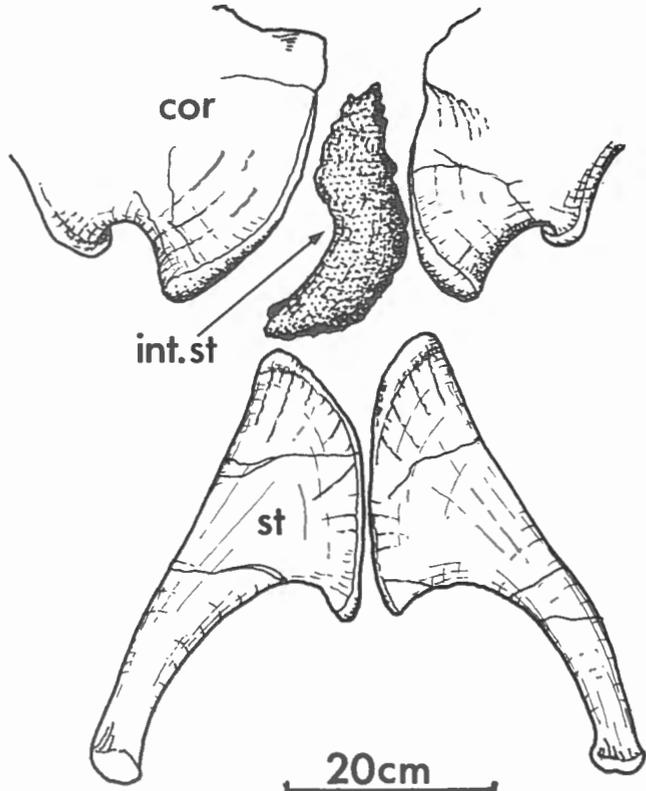


FIG. 56. — *Iguanodon bernissartensis*. (IRSNB. 1536). Sternal region of a mounted skeleton, as preserved.

From its rather irregular form and appearance, this bone is clearly not a normal part of the pectoral girdle, and for convenience it is termed an *interstitial ossification*; it presumably originated within the cartilage of the sternal plate.

In the forelimb, the *humerus* is a large, sigmoidally curved bone (fig. 57). Its proximal end is broad and antero-posteriorly flattened and has a shallow, concave

anterior (ventral) surface and a convex posterior (dorsal) surface. The centre of the proximal end has an expanded articular condyle (h - the head of the humerus) which is supported beneath by a buttress on the posterior surface of the shaft, and by a narrow shoulder on either side. The rather smooth irregular pitting on the humeral head (which indicates the presence of a cartilaginous capping) is continued along the

The dorsal surface is more complex: its proximal, medio-dorsal edge is developed into a vertical sheet of bone, lateral to which there is a shallow depression, bordered laterally by a low raised ridge. Into this depression fits the head of the radius. Farther anteriorly, the shaft of the ulna tapered before re-expanding, dorso-ventrally, near its distal end. The vertically oval distal surface is convex and articulated against the proximal carpals; along the medio-dorsal edge of this distal end there appears to be a shallow facet upon which the distal end of the radius rests.

The *radius* (fig. 58, rad) is appreciably shorter than the ulna and is a long cylindrical bone which is expanded at each end. The proximal end is rounded in end view and slightly depressed; by contrast, the distal end is, as with the ulna, dorso-ventrally expanded, with a convex articular surface which fits against the proximal carpals.

Of the numerous examples of the *manus* available, perhaps the best is that of IRSNB. 1558 (fig. 60, a, b) an isolated specimen which consists of the distal ends of the radius and ulna and the entire manus.

The *carpus* (fig. 59, a-d) is very massive in this species and the various bones within it have become fused together into two rigid blocks by a cancellous bony tissue and by ossification of the carpal ligaments (see fig. 59, sp.b; os.ligs). The proximal surface of the carpus bears large elongate depressions for the radius and ulna (fig. 59 c, ra.f; ul.f). It seems very unlikely that there would have been any significant movement between antebrachium and carpus, since the carpus is always preserved firmly attached to the radius and ulna in the Bernissart specimens. Functionally, the carpus forms a solid block of bone separating meta-

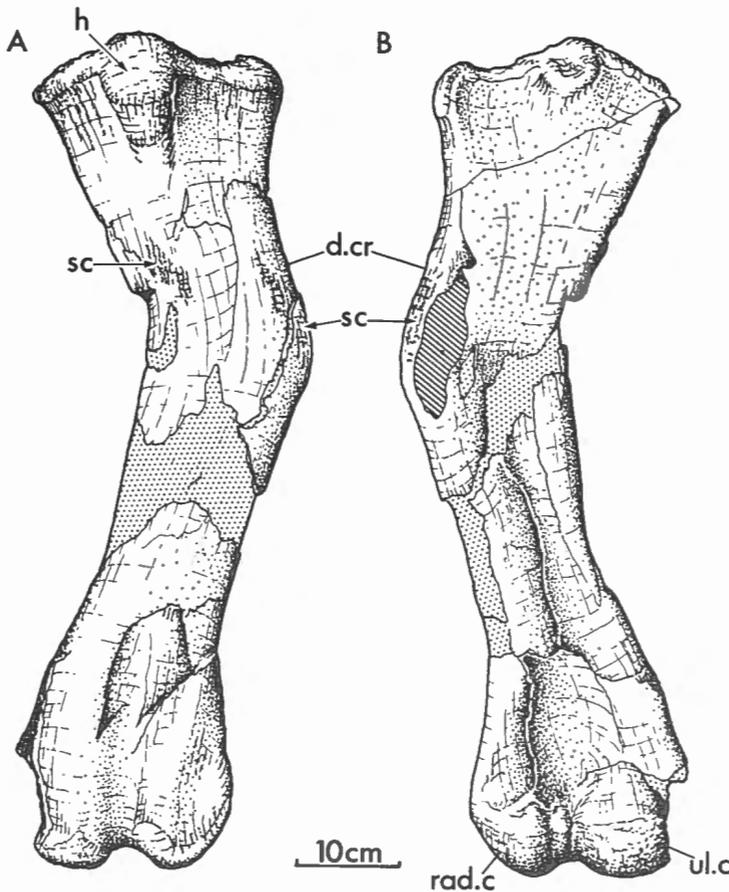


FIG. 57. — *Iguanodon bernissartensis*. (Holotype. IRSNB. 1534). Humerus (right). A: dorsal surface; B: ventral surface. Even stippling — « carton pierre »; cross-hatching — broken bone surface.

shoulders on either side, implying that they too were involved in forelimb movements. The medial shoulder overhangs the curved medial edge of the humerus, which supports the ulnar condyle (ul.c) below. From the lateral shoulder, the shaft at first drops almost vertically for a short distance before swelling outward slightly and developing a thickened, rugose edge: the delto-pectoral crest (fig. 57, d.cr). Below this crest the shaft contracts, tapering slightly toward the distal, radial condyle. The radial and ulnar condyles are separated by a shallow intercondylar groove.

The *ulna* (fig. 58, ul) possesses a large, prominent olecranon process, which is blunt and rounded, and along the dorsal surface of which the humerus articulates. Ventrally, the surface is rounded transversely, while describing a shallow sinuous curve longitudinally.

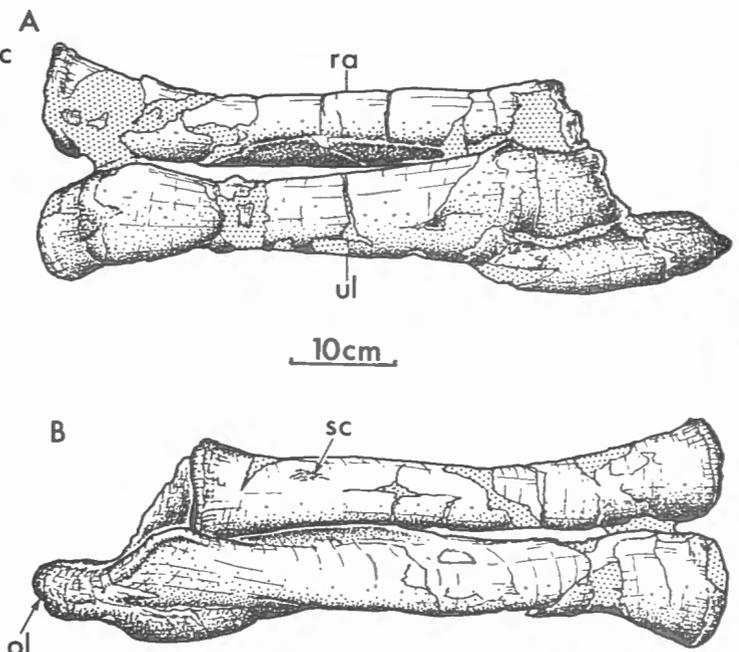


FIG. 58. — *Iguanodon bernissartensis*. (Holotype. IRSNB. 1534). Radius and ulna (right). A: medial view; B: lateral view. Even stippling — « carton pierre ».

BERNISSARTENSIS FROM THE LOWER CRETACEOUS OF BERNISSART (BELGIUM)

carpals from the antebrachium, and its distal surface is modified to receive the metacarpals. For descriptive purposes, the manus will be described as though held horizontally, with the palm facing downward.

All three proximal carpals can be identified; however, due to fusion, their detailed structure has been

flat and traversed by osseous strands, which obscure the suture between radiale and intermedium; the probable position of the suture is suggested as a low curved ridge whose position is constant and observable in several of the better preserved specimens. Laterally, this bone is sutured to the proximal edge of the ulnare

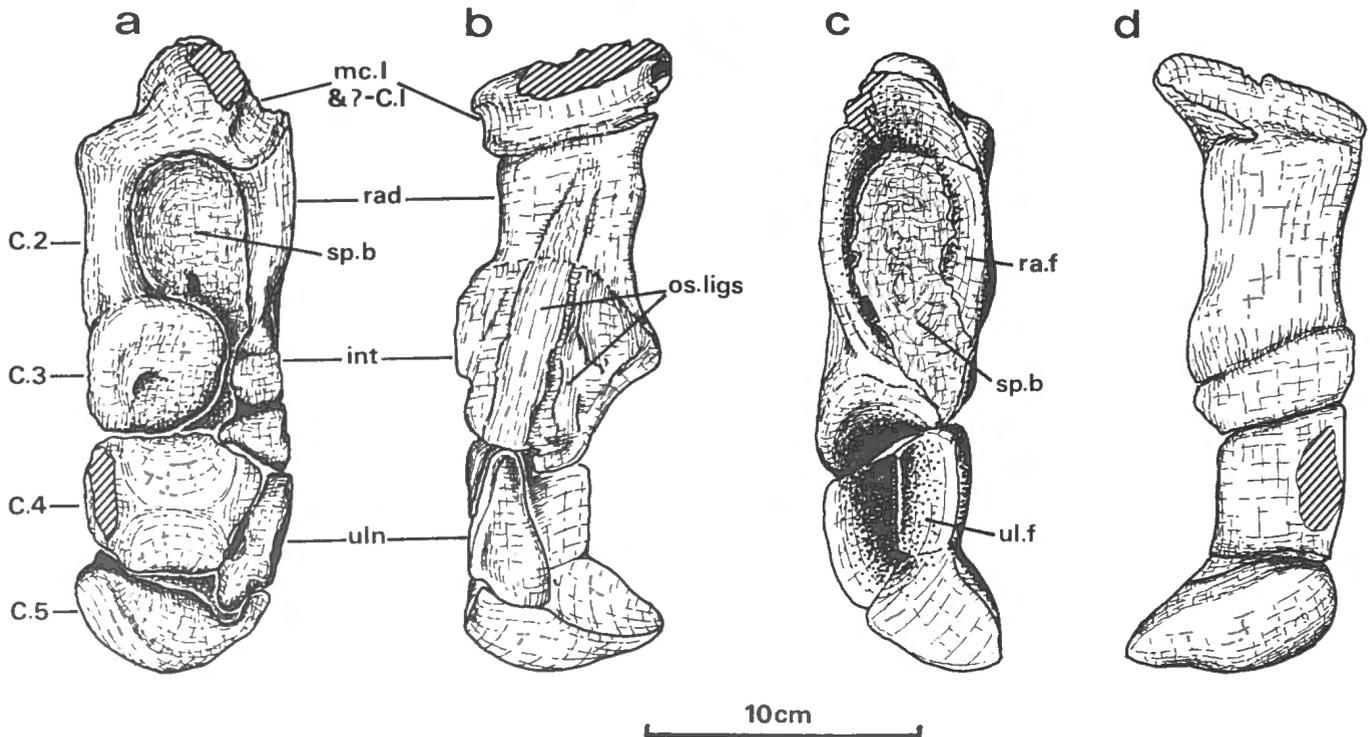


FIG. 59. — *Iguanodon bernissartensis*. (IRSNB. 1558). Articulated carpal bones. a : distal surface; b : dorsal surface; c : proximal surface; d : ventral surface.

obscured. The *radiale* (rad) is a large, block-like bone found on the dorsal wall of the carpus (fig. 59). Proximally, it forms the major part of the dorsal margin of the articular facet for the radius (fig. 59 c), while medially it is firmly fused to the base of metacarpal I — the latter having become functionally incorporated into the wrist. The external surface of the radiale is traversed by numerous, flattened, osseous strands; these appear to represent ossified strands of connective tissue, which probably helped to bind the radiale to the intermedium (fig. 59 b, os. ligs). Distally, the radiale is deeply excavated (fig. 59 a) to receive the proximal end of metacarpal II; the bone at the base of this recess has a porous appearance (fig. 59 a, c; sp.b). Medially, the distal margin of the radiale is fused to Carpal II — or so it appears, the exact relationship between these bones is uncertain.

The *intermedium* (int) lies lateral to the radiale on the external surface of the wrist (fig. 59). The proximal surface of this large bone is divisible into two adjacent concave facets : a medial one, which is continuous with the radial facet and, separated from this by an oblique ridge, is a part contributing to the ulnar facet (fig. 59 c). The dorsal (external) surface of this bone (fig. 59 b) is

and carpal IV. Its distal surface forms the external margin of the facet for metacarpal III (fig. 59 a). Ventrally, it is sutured to carpal III.

The *ulnare* (uln) is quite small compared to the intermedium and is a small, flattened wedge of bone on the external surface of the wrist, lateral to the intermedium (fig. 59). It backs carpal IV and is sutured firmly against carpal V ventrally. Its proximal surface forms a part of the large ulnar facet (ul. f - fig. 59 c).

Of the distal carpals, *carpal I* has apparently become fused to metacarpal I and cannot therefore be clearly discerned (fig. 59, mcI - CI). *Carpal II* probably forms the ventral margin of the fossa for metacarpal II and appears to be fused to the first metacarpal medially, the third distal carpal laterally, and the radiale dorsally (fig. 59 a, C2). *Carpal III* is a moderately large block-shaped element on the distal surface of the wrist, lateral to the second carpal and attached along its posterior surface to the intermedium. Its proximal surface seems almost to meet the antero-lateral corner of the radial facet, but it expands anteriorly to form a broad, rounded, button-like surface for metacarpal III (fig. 59 a). *Carpal IV* is an irregular

blockshaped element. Its distal surface is broad and bears two shallow, adjacent facets, one forming the lateral part of the facet for metacarpal III, the other forming the medial part of that for metacarpal IV. Its proximal surface forms part of the ulnar facet. *Carpal V* is an oblique, lozenge-shaped element (fig. 59, C5). Its proximal surface is concave and wraps around the ventral surface of the distal end of the ulna. Its lateral surface is oblique and convex and so allows metacarpal V to flex obliquely across the manus. A small

end forms a more or less rounded head and sits in the prominent fossa between the radiale and carpal II (fig. 59 a). The medial surface of the shaft is rounded dorso-ventrally and its edge describes a shallow concave curve as it sweeps towards the distal condyle. The dorsal and ventral surfaces are similarly shaped, but the lateral edge is flattened and irregularly marked where it was clearly bound by ligaments to the third metacarpal. The distal end of the metacarpal possesses a well defined asymmetric articular condyle, which

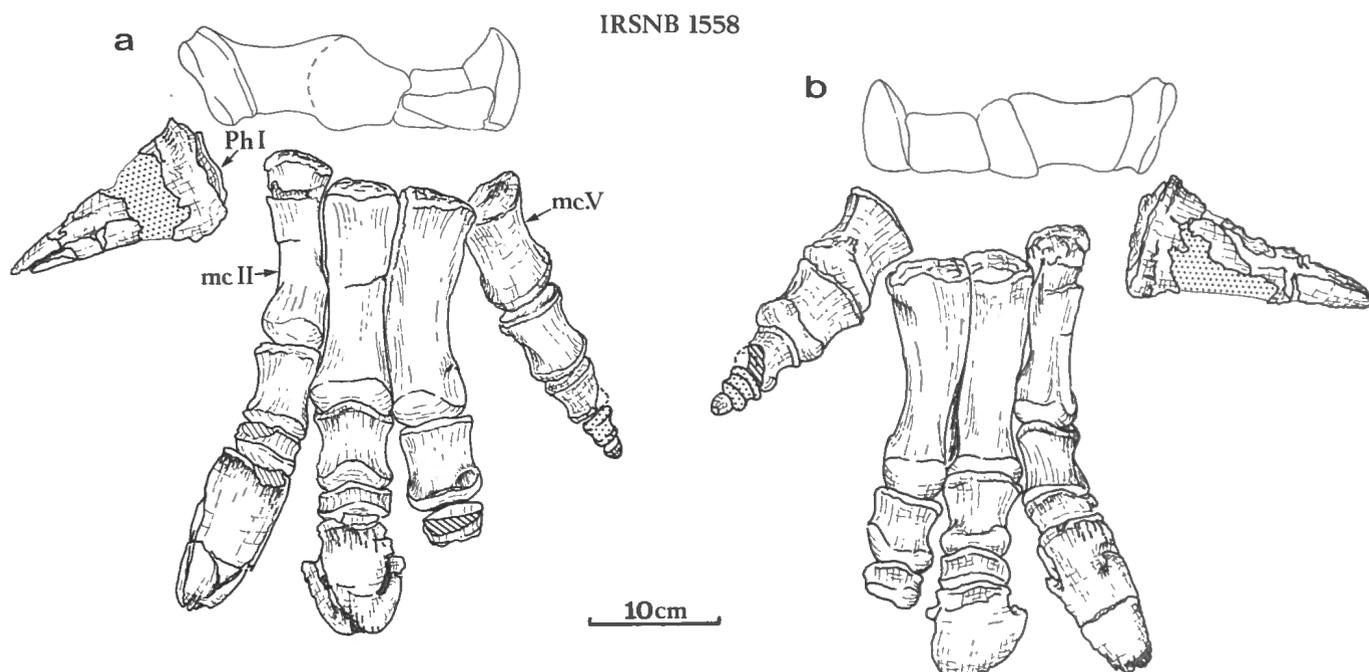


FIG. 60. — *Iguanodon bernissartensis*. (IRSNB. 1558). Articulated carpal bones. a.: distal surface; b.: dorsal surface; c.: proximal surface; d.: ventral surface.

portion of its distal surface forms the ventro-lateral edge of the facet for metacarpal IV (fig. 59 a).

Metacarpal I (figs. 59; 61 a, b) unlike the remainder of the metacarpals, has become incorporated into the carpus, being fused with carpal I and sutured along its base to the radiale and distal carpal II. The distal articular surface of this metacarpal is strongly convex dorso-ventrally, very elongate horizontally and faces obliquely antero-medially (fig. 59). Beneath the rounded articular surface, there are two broad shoulders; on the dorsal surface the shoulder ends at a slight lip which probably marks the suture with the radiale, while the ventral shoulder which is more pronounced has a less obvious suture with the second distal carpal. The distal edge of this metacarpal forms the medial margin of the fossa for metacarpal II. Proximally, the base of the first metacarpal forms a large lip which overlaps the distal end of the radius.

The *second metacarpal* has a much more typically metapodial structure (figs. 60, 61). It is of a robust, slightly dumbbell shape, the proximal and distal ends being expanded for articular surfaces, between which there is a slightly contracted, stout shaft. The proximal

extends on to the dorsal and ventral surfaces of the shaft and, ventrally, possesses a very slight flexor tendon groove.

The *third metacarpal* (figs. 60, 61) is longer than, and more stout than, the second; its proximal and distal ends are expanded while the shaft is contracted and sub-quadrangular in cross-section. In proximal view, the articular surface is approximately rectangular and feebly convex dorso-ventrally; its medial edge is slightly rounded and fits against the slightly concave lateral surface of the second metacarpal, while its lateral surface is concave to receive the medial surface of metacarpal IV. The lateral and medial sides of the shaft are heavily scarred by the powerful ligaments which held these adjacent metapodials together. The distal end of this metacarpal is expanded into a broad, symmetrical articular surface, which extends onto both flexor (ventral) and extensor (dorsal) surfaces; there is also a shallow intercondylar groove.

Metacarpal IV is the longest of the metapodials, being slightly longer than the third (figs. 60, 61). Its proximal end is broad, quadrangular and slightly con-

BERNISSARTENSIS FROM THE LOWER CRETACEOUS OF BERNISSART (BELGIUM)

vex, and articulates against carpals IV-V. In dorsal view, the shaft of this metacarpal can be seen to be curved along its length: its medial edge describing a smooth convex curve. Its entire medial surface therefore fits snugly against the adjacent third metacarpal, and is bound against the latter by ligaments. The remaining dorsal, lateral and ventral surfaces of the shaft are relatively smooth. Distally, the articular surface, which projects beyond that of the third metacarpal, is broad, convex and asymmetrical, being directed obliquely away from the centre of the palm.

that the range of articular movement between this bone, carpal V, and its proximal phalanx, was very great.

The phalangeal formula of the manus of *I. bernissartensis* is 2, 3, 3, 2, 4. Although it has been long thought that there was but a single phalanx in digit I (HOOLEY, 1925; ROMER, 1956) in fact there are two, as in most reptiles. The first or proximal phalanx (Ph. I) is a thin oval disc, which rests in a depression in the proximal surface of the cone-shaped unguis phalanx. This bone can plainly be seen *in situ* in the manus of the holotype (IRSNB. 1534, fig. 61 a, b);

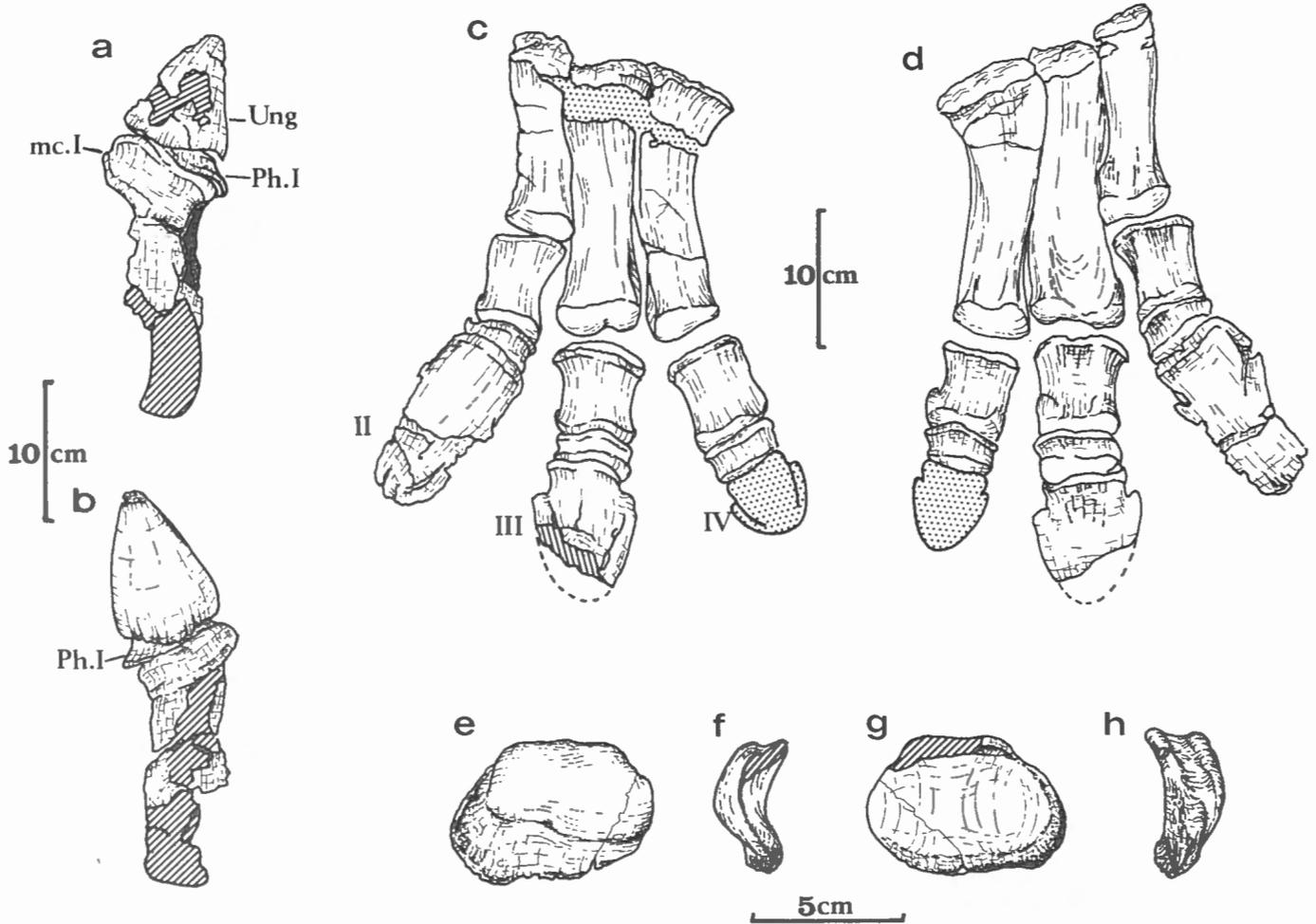


FIG. 61. — *Iguanodon bernissartensis*. (Holotype. IRSNB. 1534). Articulated carpalia and digit I in: a: dorsal; b: ventral view. Articulated digits II - IV in: c: dorsal; d: ventral view. e-h: Well preserved first phalanx of digit I found in conservatoire collection « Individu H ». e: distal view; f: medial view; g: proximal view; h: lateral view.

Metacarpal V (fig. 60) is not bound to the previous three metapodials and is considerably shorter and more stout, being approximately half the length of metacarpal III. The proximal and distal ends are expanded and between them, the shaft is moderately waisted and appears twisted along its length. The proximal end has an irregular more or less flat surface, slightly depressed at its centre; its outline is sub-circular, the ventral edge of which is flattened. The distal end is expanded and has a broad convex articular surface. The characters of the proximal and distal ends suggest

the battered remains of another are present attached to the base of the unguis phalanx of IRSNB. 1558 (fig. 60 a, b). Two isolated specimens have more recently been identified among the Brussels collections, which allow a more complete description to be made.

The first phalanx consists of a flattened convex-concave plate (fig. 61 e-h). Its proximal surface is composed of two shallow, adjacent depressions separated by a feeble broad ridge (fig. 61 g). The ventral surface is separated from the proximal surface by a

sharp sinuous ridge, and the former merges rapidly with the distal articular (?) surface. The distal surface is broad and convex (fig. 61 e); its dorsal and medial edges form prominent rounded lips which are separated by a shallow trough from the edge of the proximal articular surface. However, laterally, the proximal and distal surfaces meet at a sharp curved ridge.

for the attachment of ligaments and the tendons which controlled its movement. From its base the sides of this unguis gradually converge to a sharp apex; the whole conical structure curves ventrally, and the lateral and medial sides bear deep elongate nail grooves. Judging from the shape of the underlying unguis, the horny claw which it supported must have been

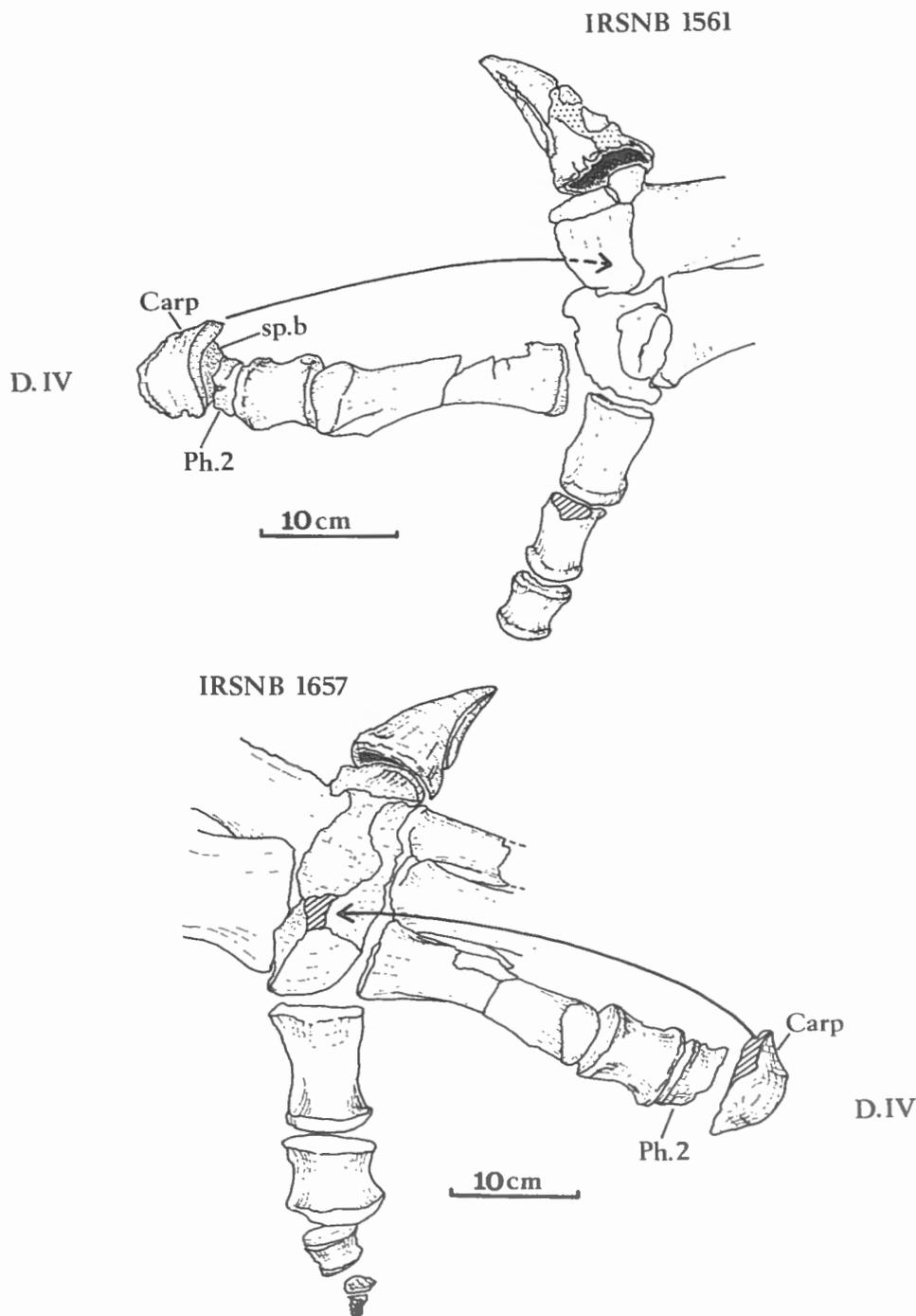


FIG. 62. — *Iguanodon bernissartensis*. The third phalanx of Digit IV.

The *unguis phalanx* of digit I is one of the most characteristic bones of the entire skeleton (figs. 60-62). Its base is broad and its proximal surface depressed; the lateral margins of its base are rugose and everted

extremely large, sickle-shaped and sharply pointed, and, if used as such, could have been a formidable weapon.

The result of the fusion of metacarpal I to the carpus has been that this digit is set at an oblique angle to

the main axis of the hand. When articulated, this digit is free to move in an oblique plane, and when flexed, describes an arc across the edge of the manus.

There are three phalanges in *digit II* (figs. 60; 61 c, d). The *proximal phalanx* is a robust block-like element; its proximal end is approximately quadrangular, depressed at its centre, with everted margins. Along the short shaft, the sides are contracted and show in cross-section a low rhomboidal outline: the dorso-lateral edge (adjacent to digit III) overhangs the ventro-lateral edge quite noticeably; this entire lateral surface is also rugose as if for ligamentous attachment to the side of the adjacent distal end of metacarpal III. The distal articular end is set at an angle, compared to the proximal surface, facing distally and slightly medially; its surface is broad and convex, with a slight intercondylar groove. Many of the Brussels specimens show this phalanx firmly attached to metacarpal III, suggesting that these two bones were normally firmly bound together by ligaments.

The *second phalanx* is a proximo-distally compressed bone, which is slightly wedge-shaped in dorsal view, being thicker laterally than medially; its proximal surface is deeply concave and the distal surface strongly convex.

The *ungual phalanx* is characteristically shaped. Its proximal end is depressed and has thickened margins. Distally, the bone tapers and becomes dorso-ventrally compressed, terminating in a bluntly rounded point. The entire unguis is twisted medially along its length, which produces a certain amount of asymmetry of its nail grooves. The medial groove is well defined and curves along the medial edge of the phalanx; the lateral groove however, curves rather irregularly across the dorsal surface of the unguis, especially toward its distal extremity.

The *third digit* comprises three phalanges (figs. 60; 61 c, d). The *proximal phalanx* is a symmetrical rectangular bone. The proximal end is roughly oblong in end view, concave dorso-ventrally with a median ridge and moderately everted margins. The short shaft is waitsted and its ventral surface scarred for attachment of a powerful flexor tendon. The distal end is expanded with a well developed articular surface which is divided by an intercondylar groove; this articular surface extends onto the dorsal (extensor) surface of the phalanx.

The *second phalanx* is very similar in general shape to that of the second digit, being strongly compressed, broad and slightly wedge-like.

The *ungual phalanx* of this digit is somewhat shorter, broader and more symmetrical than that of the second digit. Its proximal end is concave dorso-ventrally and is divided into slight, adjacent depressions by a low median vertical ridge. From the thickened articular margins, the sides of the unguis taper for a short distance before the lateral and medial edges are expanded to produce thick ledges of bone

which support each nail groove; these two ledges converge distally to produce a blunt irregular point. The main body of the unguis phalanx is dorso-ventrally flattened and both dorsal and ventral sides are rugose; the latter is exceptionally so where it serves as the insertion of a large flexor tendon.

When these phalanges are articulated together, the digit can be seen to have a slight lateral curvature. Thus digits II and III appear to splay apart, when naturally articulated. *Digit IV* has only two phalanges, unlike the closely related species *I. mantelli*, in which there are three.

The *proximal phalanx* is similar to the corresponding bone of the previous two digits, being stout and block-like; however, this bone tends to be more dorso-ventrally compressed and the articular surfaces are somewhat shallower and less clearly defined.

The *second phalanx* is a small broad element. The proximal surface is broad and depressed for articulation with the proximal phalanx. Distally, there is a very abbreviated shaft region followed by a broad, smoothly rounded, distal surface.

The « third » phalanx of this digit was erroneously reconstructed as a small nodular element by DOLLO (1882: pl. IX, fig. 3). However, several of the reconstructed skeletons: IRSNB. 1534 (the holotype) IRSNB. 1561 and IRSNB. 1657, are reconstructed at variance even with DOLLO's restoration. The holotype skeleton (IRSNB. 1534) which was figured by DOLLO (1882, 1883) has had extensive plaster restoration of the fourth digit of both left and right manus (fig. 61 c, d - stippled areas). Both, as presently restored, possess three phalanges on digit IV, the terminal one being a large, flattened, hoof-like unguis. The basis for this restoration can only have been from the evidence of the structure of the manus in specimens IRSNB. 1561, 1657; both of these appear to possess broad unguis-like bones on the fourth digit (fig. 62). Both of these specimens have since been examined in order to confirm DOLLO's original restoration. In both instances the « unguis phalanx » has proven to be an unguis-shaped fragment of bone derived from the carpus (carp) and, as indicated, these specimens can be placed in their correct positions on the carpus.

The *fifth digit* of *I. bernissartensis* is composed of four phalanges (fig. 60) in contrast to that of *I. mantelli*, which possesses only three phalanges. The first three phalanges form a tapering series, all of which are sub-cylindrical, have flattened ventral (flexor) surfaces, shallow concave proximal ends and smooth, slightly convex distal ends. The fourth phalanx however appears to show some variability in its form. In some cases it can have a blunt, broad conical appearance, with a shallow concave articular facet, while in others it can appear as a very thin convexo-concave disc-like cap perched on the third phalanx.

From the foregoing description it should be evident that the manus of *I. bernissartensis* is a remarkably specialised structure. A functional consideration of this structure has had a considerable influence on the proposals which follow concerning the probable mode of life of this species.

THE PELVIC GIRDLE AND HINDLIMB.

The *ilium* (figs. 63, 64) has a long, curved anterior process, which forms an extension of its dorsal edge. At its base, this process is triangular in cross-section (fig. 64 - shaded profile) and, following it forward, it becomes narrower and arches downward; its distal end is rather transversely compressed and twisted dorsally, ending in a rounded point. The medial side of this process possesses a thick horizontal ridge which acts as a buttress to a facet at the base of this process, against which articulates the distal end of the transverse process of the first true sacral vertebra.

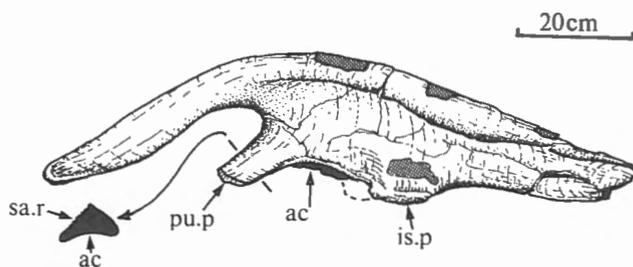


FIG. 63. — *Iguanodon bernissartensis*. (Holotype. IRSNB. 1534). Ilium (left). Lateral view.

The main part of the ilium forms a deep vertical blade; its dorsal edge is rugose, rounded and everted so that it overhangs the lateral surface of the blade. It becomes thicker and more strongly everted posteriorly (fig. 64 - shaded profile) where it forms a structure rather like an incipient form of the antitrochanter seen in the ilia of hadrosaurs. Toward its posterior end, the dorsal edge of the ilium curves downward to a rounded point. Beneath the concave lateral surface, the post-acetabular part of the ilium is reflected sharply inward and forms a broad brevis shelf, which can be clearly seen in the cross-sectioned view of this region of the ilium (fig. 64, b.sh). Anterior to the brevis shelf region, the ischiadic tuber (fig. 63), is. p) interrupts the horizontal, rounded ventral edge of the post-acetabular blade; it is expanded and has a rugose textured surface, which is flattened ventrally where it is attached to the head of the ischium. The anterior edge of the ischiadic tuber forms part of the posterior edge of the acetabulum (ac). The acetabulum forms an embayment in the lower edge of the iliac blade; its surface is cup-shaped and is bounded along its upper edge by a rim, which is particularly well-developed on the pubic peduncle (pu. p) which supports the anterior part of the acetabulum.

The pubic peduncle itself is a short stout process, triangular in cross-section, which projects obliquely forward and downward from the antero-ventral corner of the iliac blade, directly beneath the anterior process. Its ventro-lateral surface is smooth and concave, forming part of the acetabulum. A sharp ridge separates this surface from the dorso-lateral surface above. The medial surface of this process was very firmly sutured to the stout first sacral rib (fig. 63, sa. r).

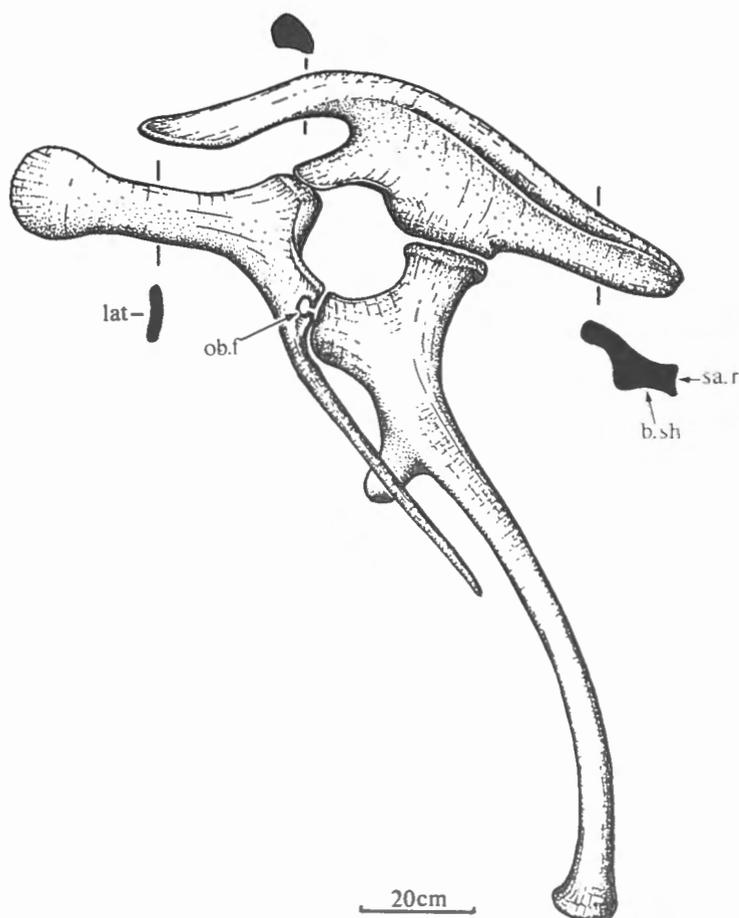


FIG. 64. — *Iguanodon bernissartensis*. Pelvic girdle reconstruction, based mainly on IRSNB. 1534.

Apart from the anterior process, very little is known of the structure of the medial surface of the ilium. Obviously the lower part of the surface bore facets for attachment of the sacral yoke. The surface above the area of sacral rib attachment is smooth, undulating and inclined laterally, running outward to meet the dorsal edge of the iliac blade.

The *pubis* (figs. 64, 65) forms the antero-ventral margin of the acetabulum and in this region it is stoutly constructed and smoothly concave. From its anterior and ventral edges, the pubis is developed into two processes: the pre-pubic and post-pubic rami. The pre-pubic ramus (an. pu) consists of a laterally compressed, slightly curved blade (fig. 65) which extends forward from the acetabular region; toward its distal end, this blade expands dorso-ventrally and

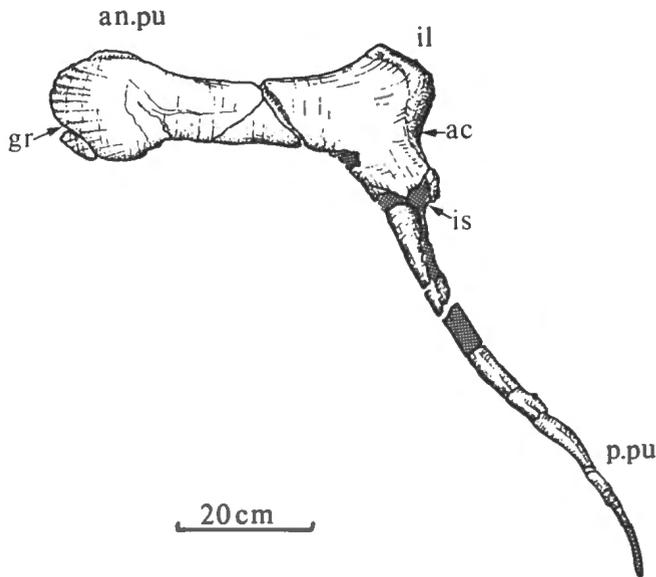


FIG. 65. — *Iguanodon bernissartensis*. (Holotype. IRSNB. 1534). Pubis (left) lateral view.

becomes rather more laterally compressed. The curved, anterior edge of this process is roughened, and its external surface is marked by a radiating pattern of ridges (gr).

Below the acetabular region, the pubis produces a narrow curved rod, the post-pubic ramus (p. pu)

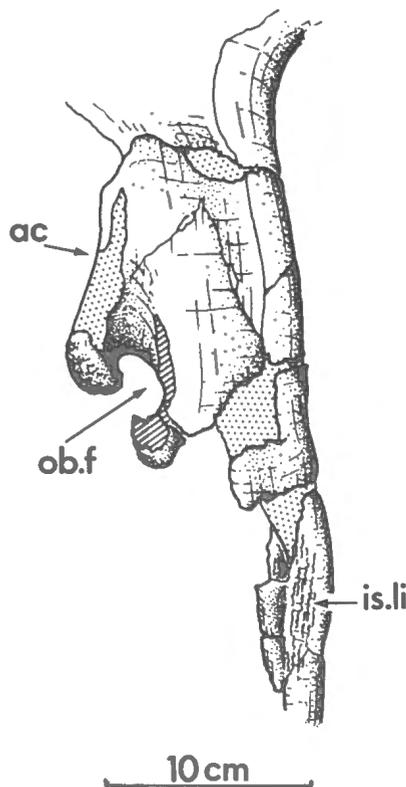


FIG. 66. — *Iguanodon bernissartensis*. (IRSNB. 1561). Medial view of the proximal end of the post-pubic ramus of the left pubis.

which curves backward and downward parallel to the ischium. Between the acetabular rim and the proximal end of the post-pubic ramus, there is an area against which the pubic head of the ischium is sutured. The dorsal surface of the proximal end of the post-pubic rod has a shallow rugose facet (figs. 64; 66, is. li) which curves dorsally along a short blunt process; this process forms the lower part of the posterior border for the obturator foramen (fig. 66, ob. f). The latter passes inward, dorsally, below and behind the acetabulum. The short blunt process referred to above is separated from the posterior edge of the acetabulum by a short

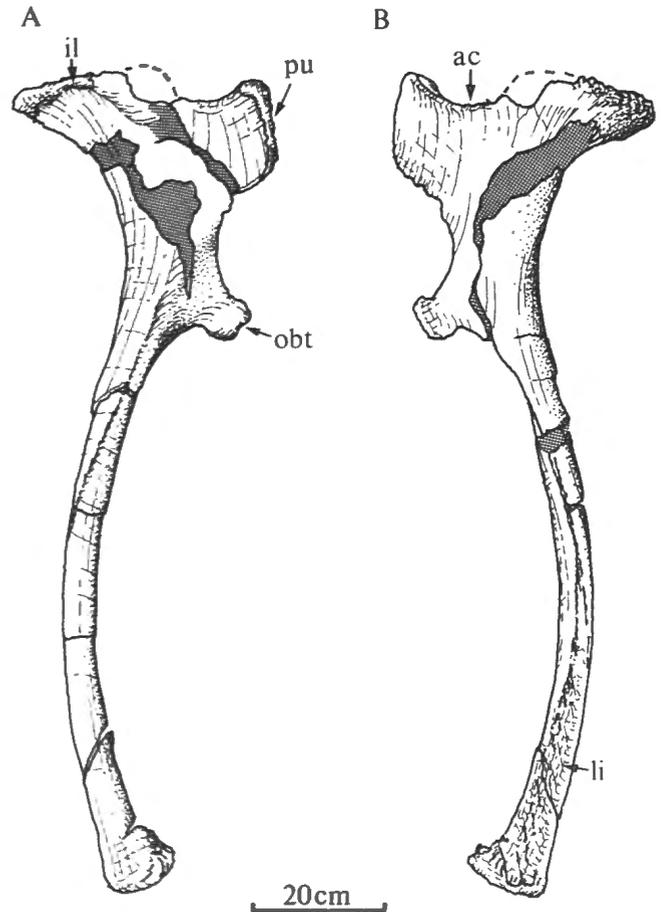


FIG. 67. — *Iguanodon bernissartensis*. (Holotype. IRSNB. 1534). Ischium (right). A : lateral view; B : medial view.

gap; this was filled by connective tissue which bound the ischium to this area of the pubis. There is no evidence to suggest that the post-pubic rami of *Iguanodon* were fused together at their distal ends as TAQUET (1976) has proposed in the iguanodontid ornithomorph *Ouranosaurus*.

The acetabulum is completed by the *ischium* (figs. 64, 67). This bone consists of a long, curved shaft, the distal end of which is slightly expanded to form a club-shaped foot; the medial surface of this end of the shaft is heavily scarred (li) indicating that it was sutured to its neighbour. Proximally, a small, leaf-

shaped obturator process (obt) is developed from the medio-ventral edge of the shaft and curves forward, medial to the post-pubic ramus. The proximal end of the shaft produces two divergent « heads » separated by a smooth, sharp-edged, embayment for the acetabulum. The anterior or pubic head (pu) is a relatively narrow flat blade which curves forward and upward to meet the pubis at its blunt anterior surface; its ventral edge is sharp and is a continuation from the base of the obturator process. Just prior to the anterior edge, the lower edge of this head develops a slightly thickened rugose surface which attached to the upper edge of the underlying post-pubic ramus. The anterior edge of the head is similarly rugose and thickened for attachment to the pubis. Toward its dorsal edge, the anterior margin becomes thicker to support the anterior portion of the acetabular rim which has a shallow articular surface continuous with that of the pubis (fig. 67 B); farther back, the acetabular rim becomes compressed to a sharp edge which curves upward to the iliac head (il). The latter is expanded, with a rugose dorsal surface which abuts against the ischiadic tuber of the ilium.

The only notable surface markings on the ischium, apart from those at the ischial symphysis, are some rugae on the external surface of the shaft, below the obturator process; these were probably an area for attachment of *M. adductores*.

The proximal end of the femur (fig. 68 a-d) is broad and saddleshaped. The head is large, globular and set

at an angle to the shaft, on a stout, short neck. The head is separated from the greater trochanter (g. tr) laterally by a narrow, waisted region. The entire proximal surface of the femur is of a uniform texture, being smooth but irregularly puckered, indicating that the whole was capped by cartilage. The external surface of the greater trochanter is scarred by vertical striations and there is a slight rounded ridge developed from its posterior half. Wrapped around the anterior side of the greater trochanter and separated from it by a narrow cleft is the lesser trochanter (l. tr). From the anterior edge of the lesser trochanter a low ridge runs down and diagonally across the dorsal surface of the shaft toward the inner distal condyle. This feature gives the shaft the appearance of having been twisted inward through 90° relative to the proximal end.

The stout, practically straight, shaft of the femur is interrupted on its postero-medial side by a thick crest of bone, the fourth trochanter (4th. tr) which has an elongate depression on the medial side of its base. The surface of the fourth trochanter and its depression are heavily scarred for attachment of powerful femoral protractor and retractor muscles. Beneath the fourth trochanter, the shaft of the femur descends to the distal condyles. The articular surfaces of these condyles are little expanded transversely but are greatly so dorso-ventrally. The two condyles are separated dorsally by a deep, almost tubular intercondylar groove (i.g) while ventrally, the condylar surfaces are extended by large heel-like buttresses which are themselves sep-

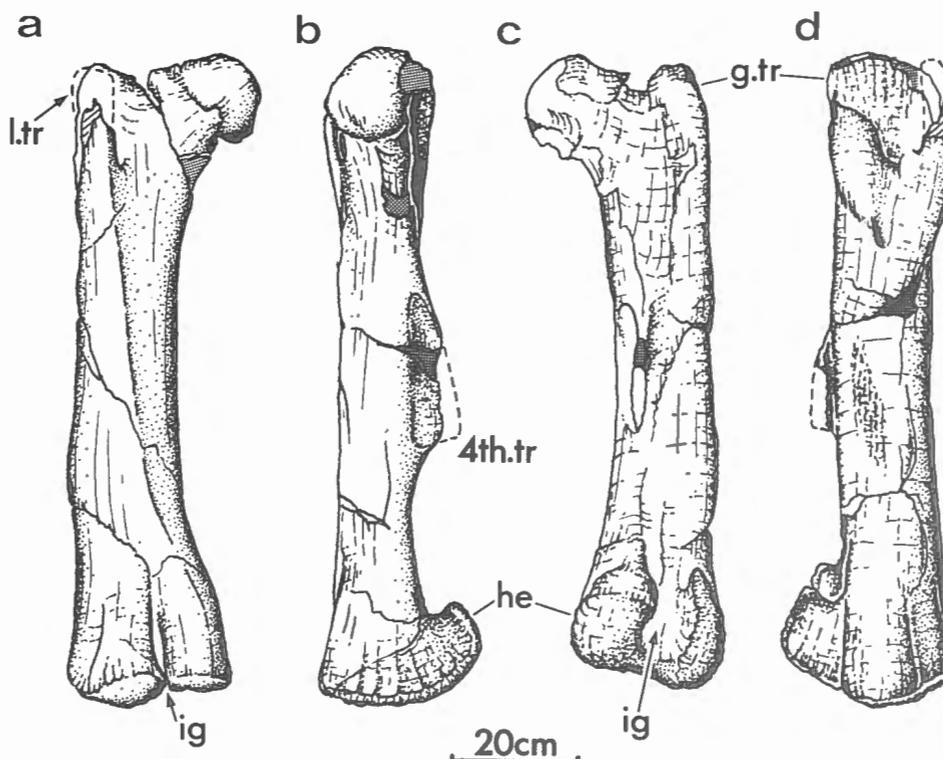


FIG. 68. — *Iguanodon bernissartensis*. (Holotype. IRSNB. 1534).
Femur (right); a : anterior (dorsal) view; b : medial view; c : posterior (ventral) view;
d : lateral view.

arated by a broad deep intercondylar groove (fig. 68 c). The external surface of the lateral condyle bears a prominent broad, vertical ridge separating the posterior heel region from the more anterior lateral surface of the condyle. The surface texture of the distal articular surfaces is similar to that seen on the proximal end, indicating a similar cartilaginous capping.

Contrary to the opinions of DOLLO (1882) the femora of *I. bernissartensis* and *I. mantelli* do not differ significantly in the positioning of the fourth trochanter. The marked differences noted and illustrated by DOLLO (1882, fig. 4) were based on incorrectly restored specimens, in which the fourth trochanter has been artificially positioned.

The proximal end of the *tibia* (fig. 69, ti) is expanded dorso-ventrally and its articular surface is more or less flat transversely and slightly convex dorso-ventrally. The head is divisible into two condyles, the lateral one having been lost in the figured example. Normally, there is a groove separating these two condyles ventrally. The outer edge of the lateral condyle articulated against the head of the fibula (*I. mantelli* - BMNH. R. 5764) and its dorsal edge is extended and curves laterally around the dorsal edge of the fibula as a large cnemial crest (fig. 69 a, cn). The inner condyle has a convex medial edge, and is somewhat larger than its neighbours. Distally, the tibial shaft contracts toward its middle before re-expanding to form the malleoli against which the proximal tarsals articulate. The malleoli are transversely expanded and are separated by a step (*I. mantelli*, BMNH. R. 6433) which separates the astragalus and calcaneal facets.

The lateral malleolus (lm) bears on its anterior surface a scarred area, above the calcaneal facet, against which the fibula was ligamentously bound. The proximal tarsals form caps of bone which are immovably bound to the malleoli and fibula.

The *fibula* (fig. 69) is a narrow elongate bone. Its proximal end is dorso-ventrally expanded and lies against the outer condyle of the tibia. Below this, the shaft tapers toward the distal end, where it re-expands to produce a blunt-ended foot, which rests on a facet on the proximal surface of the calcaneum (fig. 69 d); its medial surface is bound to the lateral malleolus of the tibia.

The ankle of *Iguanodon* is constructed so that the hinge is of a meso-tarsal type (a simple transverse hinge between the proximal and distal tarsals). As a result, the proximal tarsals are wrapped around and firmly bound to the tibia and fibula, while their distal surfaces form a broad, saddle-shaped articular surface. The distal tarsals are similarly firmly lodged against the proximal ends of the metatarsals forming a discontinuous articular surface of flattened discs, which acted as thrust pads.

The *astragalus* (fig. 69, as) is the larger of the two proximal tarsals, capping almost the whole of the distal surface of the tibia and forming most of the smooth saddle-shaped articular surface. Its proximal surface (*I. mantelli*, BMNH. R. 5354) is excavated to receive the tibial malleoli. A broad ascending process is developed from its dorsal edge (fig. 69) which wraps around on to the dorsal surface of the tibia and presumably helped to reduce the tendency of this bone to rotate

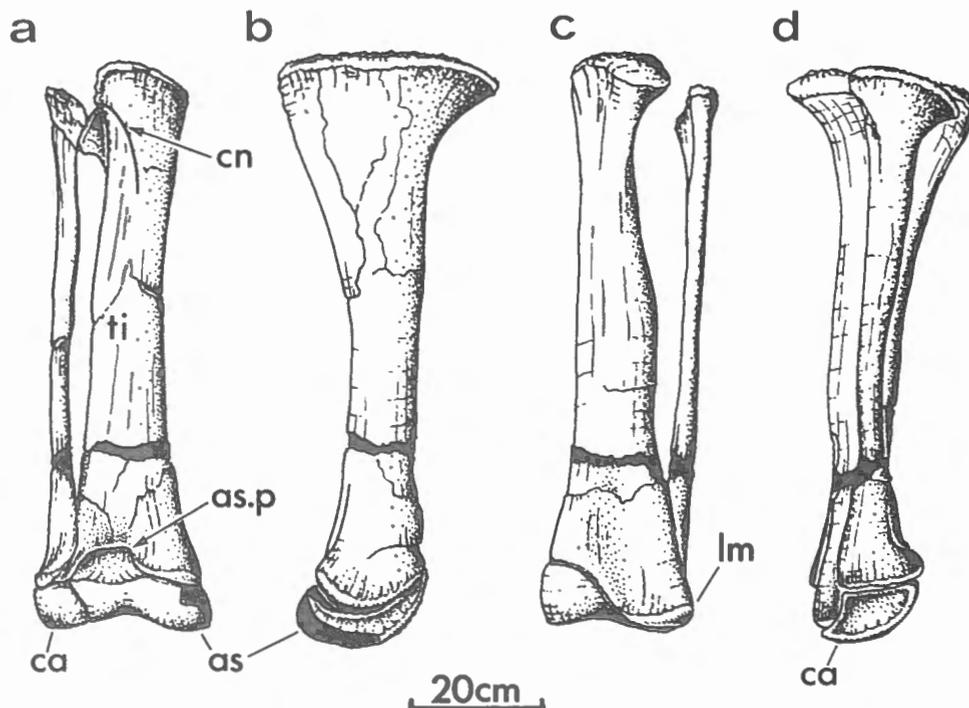


FIG. 69. — *Iguanodon bernissartensis*. (Holotype. IRSNB. 1534).
Articulated cruro-tarsus. a : anterior (dorsal) view; b : medial view; c : posterior (ventral) view;
d : lateral view.

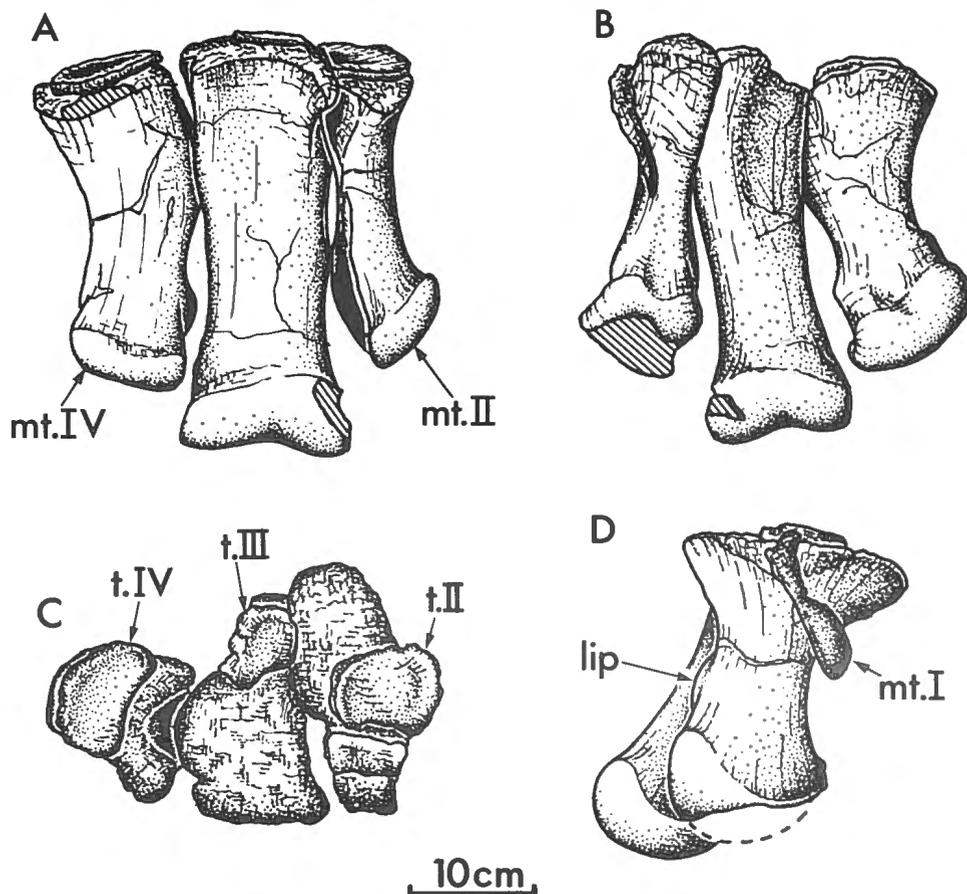


FIG. 70. — *Iguanodon bernissartensis*. (Holotype. IRNSB. 1534).
Articulated distal tarsals and metatarsals. A : anterior (dorsal) view;
B : posterior (ventral view); C : proximal view; D : medial view

against the malleoli when the ankle was flexed. At the base of the ascending process there is an undulating ridge which marks the dorsal limit of the meso-tarsal joint.

The *calcaneum* (fig. 69, ca) is a relatively narrow bone forming the outer edge of the proximal part of the meso-tarsal joint. Its distal surface is convex dorso-ventrally and slightly rounded transversely. Its proximal surface is divided into two facets, separated by a step: a dorsal portion on which the foot of the fibula rests, and a ventral portion which wraps around the edge of the lateral malleolus (fig. 69 d). The junction between astragalus and calcaneum is not known precisely but seems to have been a relatively simple flat-edged junction.

Although firmly attached to the crus, the proximal tarsals never seem to become fused either to each other, or with the crus, even in the largest of specimens.

Three distal tarsals have been identified in *I. bernissartensis* (fig. 70 C, t. II - IV); each is found attached to the proximal end of a metatarsal.

Distal tarsal II is rather imperfectly preserved in the holotype (fig. 70 C, t. II) but the fragments which remain indicate that it was a relatively thin plate of bone attached to metatarsal II. The proximal surface

of tarsal II has a smooth, undulating articular appearance.

Distal tarsal III (fig. 70 C, t. III) appears to have been smaller than tarsal II and seems to have been located near the ventral edge of the proximal surface of metatarsal III; at least, the remains of this tarsal are found in this position in both left and right pes. The proximal surface appears to have been more or less planar and smooth, with rugose edges.

Distal tarsal IV (fig. 70 A, C, t. IV) is well-preserved in many specimens of this species. It is a relatively thin convexo-concave, kidney-shaped disc of bone, the convex lower surface of which was received into a recess on the proximal surface of metatarsal IV. The edges of its proximal surface are raised and slightly irregular, but its centre is smoothly depressed.

There are four metatarsals in the pes (fig. 70, 71) all of which are bound together into a broad metapodial unit. Of these four, three (II, III and IV) are functional: that is, they support phalanges, while the remaining one (I) is reduced to a flattened splint alongside metatarsal II.

Metatarsal I (mt. I) is quite well-preserved in several specimens (fig. 70 D). As can be seen, it is a short, flattened rod applied to the medial side on the proximal

end of metatarsal II and points obliquely ventro-distally.

Metatarsal II (fig. 70 A - D, mt. II) is considerably larger than the first, although it is the smallest of the remaining metapodials; its proximal end is laterally compressed and dorso-ventrally expanded, so that it considerably overhangs its shaft. The proximal surface is more or less flat, with a slight convexity dorsally and ventrally. Distally, the shaft is strongly contracted and curves dorsally to its expanded distal articular condyle. The proximal half of the lateral surface of the shaft is flattened and scarred where it is attached to metatarsal III; about halfway along its shaft, there is a small lip-like projection from the latero-dorsal surface (fig. 70 D) which appears to have reinforced the attachment between metatarsals II and III. Beneath this lip, the shaft diverges from metatarsal III. The distal articular surface is large, well-defined and faces obliquely inwards; its ventral edge has a slight intercondylar groove which probably acted as a pulley to guide a powerful phalangeal flexor tendon.

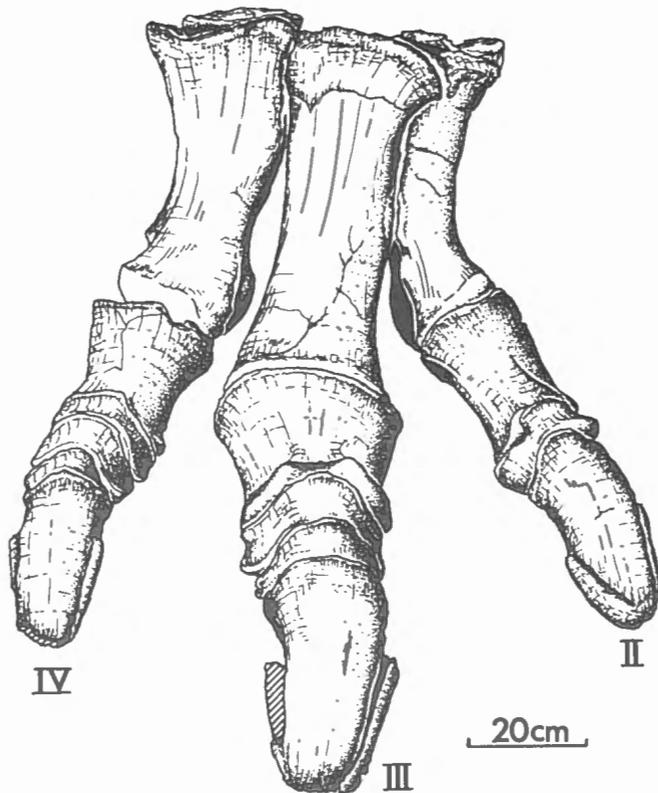


FIG. 71. — *Iguanodon bernissartensis*. (Holotype. IRSNB. 1534). Pes (right). As preserved (from photograph).

Metatarsal III (fig. 70, mt. III) is the largest and most symmetrical of the metapodials. Its proximal end is expanded and irregularly triangular, with its apex ventral. Both sides of the shaft of this metatarsal are heavily scarred by ligaments. Distally, the shaft expands into a large saddle-shaped articular condyle.

Metatarsal IV (fig. 70, mt. IV) again has an expanded proximal end, the medial edge of which is

recessed where it fits against metatarsal III, while its lateral edge is rounded. The proximal surface is cup-shaped to receive distal tarsal IV. Beneath the head, the shaft is contracted and its medial side bears a ligamentously scarred ridge, which extends about half-way down the shaft. Beyond this ridge, the shaft curves laterally, away from metatarsal III, before ending in an oblique, rounded articular condyle; the ventral edge of this condyle has a slight intercondylar groove similar to that noted in metatarsal II.

The phalangeal count of the pes is : 0, 3, 4, 5, 0 (see fig. 71). The proximal phalanges of the three digits are of similar form (fig. 72, pro) being relatively massive, block-like elements with broad concave proximal surfaces and similarly broad, but saddle-shaped distal surfaces. The proximal half of the ventral surface of each phalanx has a large, flat, scarred area for insertion of powerful flexor tendons (fig. 72, F. te).

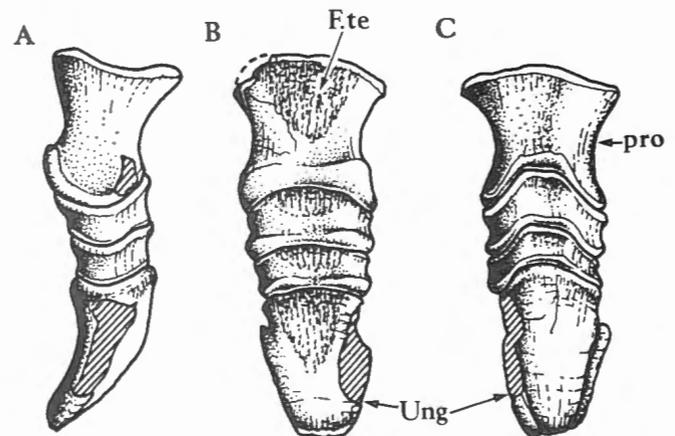
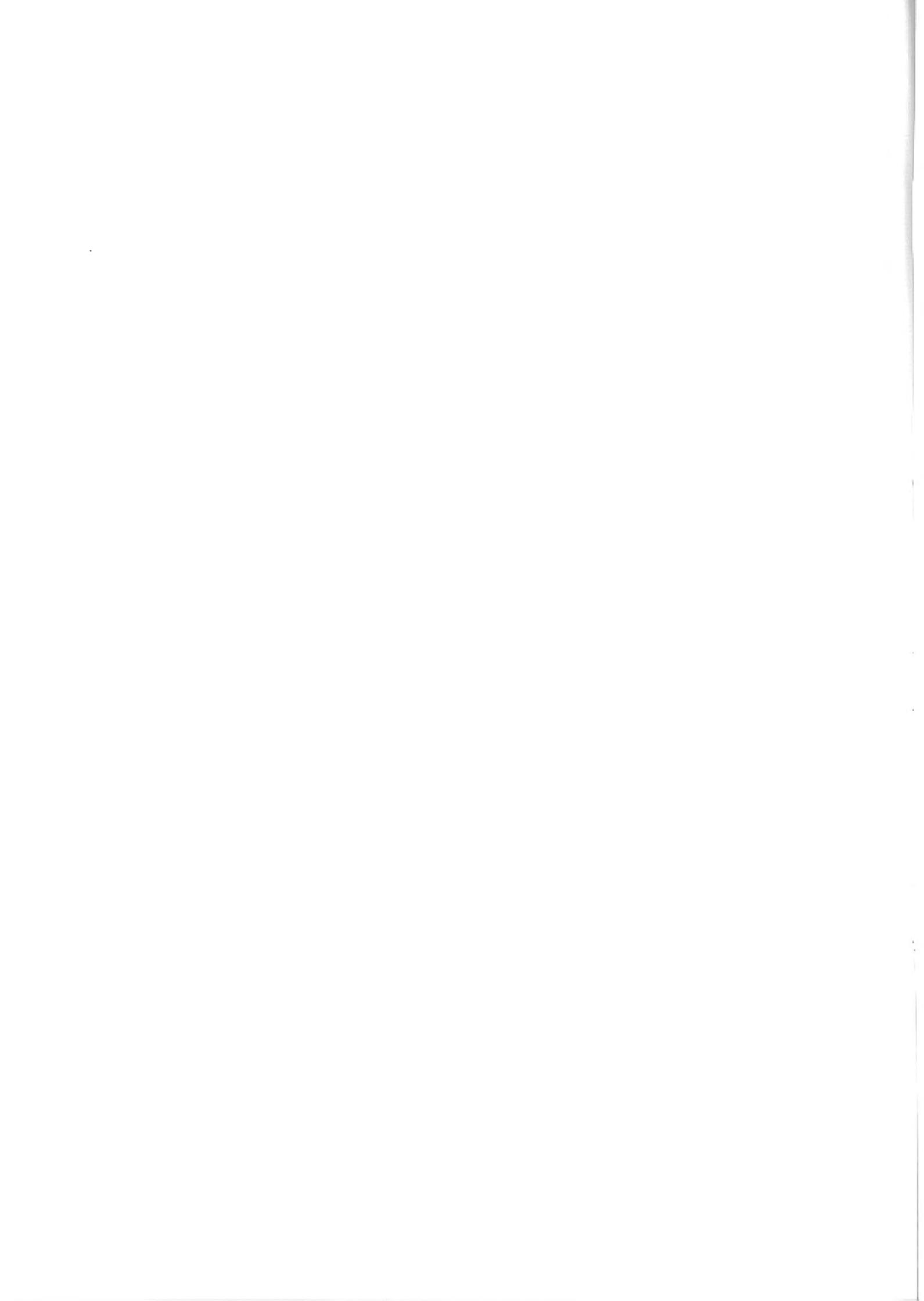


FIG. 72. — *Iguanodon bernissartensis*. (Holotype. IRSNB. 1534). Digit III of pes. A : lateral; B : ventral; C : dorsal.

The middle series of phalanges i.e. those between the proximal and ungual phalanges (figs. 71, 72) are all relatively short, broad convexo-concave plates of bone which get progressively smaller distally. The proximal and distal articular surfaces are well-developed with slightly everted margins: the former are concave, with a median ridge separating two depressions, whereas the latter are convex and saddle-shaped.

The ungual phalanges are large and hoof-like (fig. 72, Ung) being slightly arched and dorso-ventrally flattened toward their tips. The ungual phalanx of digit III is symmetrical, with well-developed claw grooves running along either side and converging on the rugose distal edge of the ungual. The unguals of digits II and IV are both twisted away from digit III and reflect the normally splayed arrangement of the toes (fig. 71); this is particularly noticeable in the asymmetry of the claw grooves.



D — ANATOMICAL OBSERVATIONS

CRANIAL.

The Horny Beak.

There is no direct evidence, in the form of preserved material, for the presence of a horny beak in *Iguanodon*. However, there are several facts which not only imply the presence of such a beak, but also make it a necessity. Firstly, impressions of horny beaks have been preserved and described in several of the quite closely related hadrosaurian dinosaurs: *Anatosaurus* (COPE, 1883; VERSLUYS, 1923), *Corythosaurus* (STERNBERG, 1935). Unfortunately all of these specimens have been reported as either lost or destroyed. More recently a newly discovered specimen of *Anatosaurus* possessing a mould of the upper beak has been described by MORRIS (1970). Secondly, there is evidence from the preserved bony tissue associated with the beak region of *Iguanodon*. The upper and lower beaks were supported by the premaxillae and prementary respectively. The occlusal margins of both of these bones are edentulous, contrary to the opinion of CASIER :

« Cet élément osseux [prementary]... n'est pas totalement dépourvu de dents. Non seulement d'importantes aspérités osseuses en ornent le bord oral, mais on y trouve latéralement des rudiments de vraies dents... incomplètement émergées du tissu osseux ».

(E. CASIER, 1960 : 42)

They are also heavily scarred and pitted in similar fashion to the bone underlying the horn-covered jaws of chelonians, as well as the claw — bearing ungual phalanges of the digits of *Iguanodon*. Naturally, since the beak area would have been the principal feeding structure it would have been liable to considerable abrasion; some form of covering is therefore necessary to protect the dermis from infection.

The general morphology of the premaxillae and prementary offer some evidence of the probable shape and characteristics of the beak. The external surface of each premaxilla is covered by irregular markings, which extend forward along the lateral rim which runs beneath the external naris (fig. 2) and upward along the median dorsal process which separates the nares (fig. 3); these rugae decrease in prominence farther back along this process. Internally, the buccal surface of the premaxillae is similarly rugose and pitted. Clearly, these areas represent surfaces upon which the horny beak grew and to which it was attached.

The occlusal edge of the premaxillae is divisible into two zones: anteriorly, the margin is sharp-edged and developed into small but regularly spaced projections, behind which are a row of shallow vertical grooves (fig. 5, gr); postero-laterally, along the sides of the premaxillae the sharp occlusal edge declines and develops a broader, rounded edge (fig. 5). The opposing prementary is broad and U-shaped in occlusal view (fig. 15). Its entire external and upper internal surface has a rough texture. Several vascular foramina (v. for) perforate the lateral portions of the occlusal edge and, in addition, several large vascular foramina are found along the anterior edge of the dentary, indicating a rich vascular supply to the growing area of the prementary beak (figs. 2, 15). The anterior margin of the prementary is sharp and is produced into several large conical projections (figs. 9, 15). These decline in height laterally and produce a low undulating ridge along the lateral edges of the prementary. Medial to this ridge, there develops a broad shelf which becomes wider posteriorly.

It would seem reasonable to suppose that the shape of the underlying bone influences the shape of the horny beak that it supports. Applying this very general principle to the structure of the beak of *Iguanodon*, it would seem that it probably had a rather specialised structure. Anteriorly, the sharp edges of the premaxillae and prementary indicate a similarly sharp-edged beak. Laterally and posteriorly, these sharp edges decline to produce a broad, rounded edge to the premaxillae and a broad shelf bordered externally by a ridge on the prementary; this indicates a flat, pad-like edge to the premaxillary beak and a broad pad bordered by a raised ridge on the prementary. The bony projections on the anterior margins of the upper and lower beaks, although undoubtedly playing a supporting role, must also have produced a rather jagged cutting surface to both occlusal margins. In this connection, the inner surfaces of the premaxillae appear to show some evidence of beak occlusion. The grooves and fossae behind the occlusal edge correspond exactly with the bony projections of the prementary and seem to represent wear facets (see fig. 9).

These apparently jagged anterior edges of upper and lower beaks would have formed an extremely effective cropping device, suitable for a range of plant food: from bark and woody stems to pine needles, leaves and soft vegetation. Like the incisor teeth of rodents, the horny beak has the advantage of being self-sharpening and rapidly replaced. The lateral and posterior portions of the beak seem, perhaps, to be

modified for a crushing and/or grasping function for tearing, rather than cutting larger pieces of vegetation prior to mastication. From the evidence available, the beak of *Iguanodon* seems to have been adapted for a primarily browsing function.

HADROSAUR BEAKS. — Ever since the description of the remains of *Hadrosaurus* (LEIDY, 1858) the mode of life of hadrosaurs i.e. whether they were aquatic or terrestrial animals, has been a contentious point. To this end, the structure of the horny beak of hadrosaurs has been investigated on several occasions, in the hope of shedding further light on their foraging abilities and thus providing indirect evidence on their preferred habitat.

In favour of an aquatic mode of life have been: ABEL (1912) who first suggested that the beak constituted a truly duck-like bill, which was used for mud-grubbing in swampy environments; these views have since been modified by MORRIS (1970) after detailed studies on the beak of *Anatosaurus*. MORRIS proposed that the hadrosaur beak was a very thin structure and therefore intrinsically too weak for foraging on vegetation. The internal surface of the beak was grooved and MORRIS proposed that this represented an adaptation for filter feeding. In contrast VERSLUYS (1923) proposed that the beak of hadrosaurs would have been ideally suited to foraging for leaves and bark, while more recently OSTROM (1961) reconsidered the function of the hadrosaur beak and, although favouring a terrestrial mode of life for hadrosaurs, conceded that the beak could have been used for both terrestrial foraging and as a scoop for aquatic vegetation.

Considering the general morphology of the jaws of hadrosaurs, the jaws are stout and have massive batteries of interlocking teeth adapted for grinding, the jaw articulation is « off-set » from the occlusal plane, the coronoid process is well-developed and the temporal region of the skull is deep. All these features suggest that the jaw action was powerful and used for grinding resistant plant fibres. Parallel adaptations can be seen in present-day herbivorous ungulates which have similarly massive jaws, complex grinding teeth, powerful jaw adductors and an elevated (off-set) jaw articulation. To my mind one of the most relevant pieces of evidence regarding the diet of hadrosaurs, is the analysis of the preserved stomach contents of *Anatosaurus* by KRAUSEL (1922); this revealed the presence of conifer needles and other fragments of terrestrial plants, which certainly seems to be in accordance with the morphology of the jaws and supports the view of a terrestrial foraging existence.

Considering the proposals for aquatic feeding by hadrosaurs of ABEL and MORRIS, there appear to be a number of at least questionable points. If, as MORRIS suggests, the beak was used for mud-grubbing and filtering out invertebrates, then there are normally two ways of dealing with this type of food: either, the food is swallowed whole (e.g. some cetaceans) or the exo-

skeletons of the prey are cracked open using flat, crushing teeth (e.g. placodontids, some skates and rays, etc.). The powerful jaw apparatus of hadrosaurs suggests that the latter method may have applied. However the grinding instead of simple vertical crushing action of the jaws would have been just as likely to damage the teeth as to pulverise the calcareous exoskeletons. Secondly, if hadrosaurs were feeding on aquatic plants, then the allegedly weak beak, with its « filtering » arrangement becomes inexplicable and the powerful jaw apparatus rather unnecessary; many animals which feed on aquatic plants tend not to have a powerful grinding dentition since aquatic plants are mostly succulent.

The evidence of the structure of the beak and jaws would seem therefore to favour a terrestrial foraging existence for hadrosaurs. The peculiar grooving on the internal surface of the upper beak of *Anatosaurus* which led MORRIS to propose a filter-feeding function, may have an alternative explanation. The grooves could represent wear facets created by abrasion against the leading edge of the prementary beak. This proposal, in turn, implies that the lower beak margin was serrated or had a series of tooth-like projections similar to those already noted in *Iguanodon*. Evidence to support this claim is found in the descriptions of a few hadrosaur prementaries (LAMBE, 1920; PARKS, 1923; GILMORE, 1933; OSTROM, 1961) all of which describe hadrosaur prementaries with crenulated margins (see GILMORE, 1933 : fig. 28; OSTROM, 1961 : fig. 17). It seems likely therefore that the horny beak, in some hadrosaurs at least, was denticulate and could have produced a series of grooved wear facets on the internal surface of the upper beak whilst feeding.

The Tongue.

The tongue of *Iguanodon* has been the subject of much speculation ever since MANTELL (1848) first suggested, albeit tentatively, that the anterior end of the mandible was spout-like in order to accommodate a

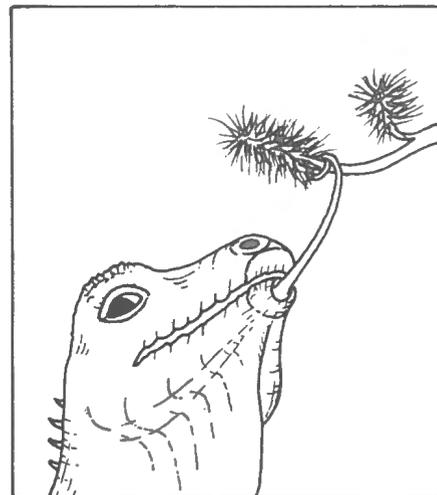


FIG. 73. — The prehensile tongue of *Iguanodon*. Redrawn from HEILMANN (1928, fig. 3).

large, muscular, prehensile tongue. This was, however, before it was realised that the spout-like symphyseal region of the mandible received the predentary bone. Much later, in 1923, DOLLO considerably amplified MANTELL's original proposal. He considered that *Iguanodon* represented the reptilian equivalent of the giraffe, and that by analogy with the giraffe, it possessed a long, narrow, prehensile tongue, with which it would browse on arboreal foliage. To support this proposition, DOLLO illustrated the predentary and lower jaws of a Bernissart specimen (IRSNB. 1561) in which he described a small aperture in the anterior wall of the predentary, the « ouverture pyriforme » (DOLLO, 1923 : 70). This discovery so influenced HEILMANN that in 1928, shortly after his « Origin of Birds » restoration of *Iguanodon* in 1926, he published a new restoration of *Iguanodon* in a very upright pose, accompanied by a close-up sketch of the alleged prehensile tongue (fig. 73). The specimen in which DOLLO located the « ouverture pyriforme » has been re-examined, as were the many other skulls in the collections in Brussels : no opening was found. The alleged opening (DOLLO, 1923 : pl. 4, fig. 3, « o ») was merely an artefact produced by an area of fracturing in the predentary.

With regard to the evidence for the structure of the tongue in *Iguanodon*, there are two features of the skull which indicate its form and probable function. These are the development of the hyoid apparatus and the morphology of the beak.

The hyoid apparatus is represented by the paired 2nd ceratobranchials, which are large and well ossified (fig. 17). As the muscles which operate the tongue are attached to the hyoid apparatus, it seems reasonable to assume that a well-developed hyoid implies a strongly muscularised tongue (OSTROM, 1961). Since *Iguanodon* also masticated its food, it seems perfectly reasonable that a large muscular tongue should have been present to move food around within the mouth. However, this does not reveal whether or not the tongue was prehensile.

Additional indirect evidence bearing on this point is that the beak area of *Iguanodon* was well-developed and undoubtedly covered by a horny sheath which probably bore sharp, serrated cutting edges. Theoretically at least, such a beak would have formed a very effective cropping device obviating the need of a prehensile tongue.

Supraorbitals (Palpebrals).

The supraorbitals are enigmatic bones, which are very well-developed in *Iguanodon*. As in most ornithischians, these bones are elongate and taper distally from a broad base which articulates against the anterior orbital margin. However, instead of projecting diagonally across the orbit, as is usually the case in Ornithopoda, they arch upward, following the dorsal margin

of the orbit before terminating lateral to the postorbital (figs. 2, 11).

Both COOMBS (1972) and more recently TAQUET (1976) have commented on the structure of the supra-orbital bones of *I. bernissartensis* and have suggested on the basis of DOLLO's figures (1883), firstly that the supraorbital articulated with both prefrontal and lachrymal and secondly, that the accessory supraorbital (So. 2) was an artefact resulting from post-mortem fracturing. Both of these claims are incorrect. It is generally believed that *Iguanodon* had a single supra-orbital, as was demonstrated for *I. mantelli* (*I. atherfieldensis*) by HOOLEY (1925). However, the bone described by HOOLEY as the « supraorbital » is in fact the prefrontal; no supraorbital was preserved with this skull.

The function of the supraorbitals of *Iguanodon* is not immediately obvious. They form prominent brow ridges which are firmly though not immovably bound to the skull. Their very prominence makes it at least conceivable that they may have had some function related to intraspecific behaviour : perhaps providing protection for the eye during combat of a head clashing or head-to-head pushing type, or alternatively supporting some sort of visual display structure. These however are mere speculations and have in general been inspired by the recent work of HOPSON (1975) on the possible behavioural adaptations of ornithopod dinosaurs.

The occiput.

GALTON (1974) suggested the need for more information which can be used to ascertain whether the paroccipital process of ornithischians is usually formed by the opisthotic or by the exoccipital.

The entire occipital surface of *I. bernissartensis* is rather poorly preserved. Nevertheless several cranial fragments shed some light on the construction of the occiput in this species. The exoccipitals form pillars on either side of the foramen magnum and meet above and below this opening, thereby excluding the supra-occipital and basioccipital from its borders. The lateral walls of the exoccipitals, which are pierced by several foramina, appear to contact the opisthotic around the point of emergence of the Vagus foramen (BMNH. R. 2501). On either side the exoccipitals expand into the large paroccipital wings. Several specimens (IRSNB. 1561, 1535, 1562, 1680) do not show any clear sutural lines between exoccipital and opisthotic. However, the rather well-preserved occiput of the right half of the specimen (IRSNB. 1536 : fig. 8) appears to show the exoccipital as a thin, wing-like plate which backs on to the paroccipital wing proper. It is possible either that the suture noted in IRSNB. 1536 is an artefact produced by *post-mortem* displacement, or that or that complete fusion along this suture had not yet

occurred, or even that the degree of fusion of the exoccipital and opisthotic was variable.

In *Hypsilophodon*, the structure of the occiput is rather interesting. GALTON (1974 : 22) described the exoccipital as a small element forming « ... the ventrolateral border of the foramen magnum while the round posterior surface forms part of the occipital condyle ». This bone is not indicated in occipital view (*loc. cit.* fig. 8). The restriction of the exoccipitals to relatively small elements is rather unusual, since the line of contact between opisthotic and exoccipital in reptiles normally occurs at the Vagus foramen on the lateral wall of the braincase at the position of the fissure between otic and occipital cartilages (ROMER, 1956). Since the latter situation is found in *Iguanodon*, it is wondered whether the exoccipital suture described by GALTON (*loc. cit.* fig. 9 B.C.) is not an artefact and the exoccipitals and opisthotics are indistinguishably fused. In this context, it is interesting to note that JANENSCH (1955) failed to locate an opisthotic-exoccipital suture in the closely related ornithopod *Dysalotosaurus*.

In *Camptosaurus* (GILMORE, 1909) the exoccipital and opisthotic are regarded as firmly fused. GALTON (1974 : 105) states that GILMORE « ... regarded the portion forming the occipital condyle as exoccipital and the rest, including the paroccipital process, as opisthotic ». Thus GALTON would have the construction of the occiput of *Camptosaurus* just as he proposed for *Hypsilophodon*. However what GILMORE in fact said was :

« The exoccipitals from the greater part of the boundary of the foramen magnum and contribute slightly to the formation of the occipital condyle. ... articulating dorsally with the supra-occipital, and continuing latero-posteriorly into the broad opisthotics or paroccipitals ».

(C.W GILMORE, 1909 : 207)

A similar conformation of the occiput and paroccipital process to that described in *Camptosaurus* has been reported in other « iguanodontids » (*sensu* GALTON) : *Tenontosaurus* (OSTROM, 1970) *Ouranosaurus* (TAQUET, 1976).

Among the hadrosaurs, the paroccipital wings appear to be formed exclusively of the exoccipitals. An isolated exoccipital of *Bactrosaurus* was figured by GILMORE (1953 : fig. 23) and a very similar exoccipital appears to have been present in *Lophorhynchon* (LANGSTON, 1960 : fig. 153). However, owing to fusion, the contribution made to the paroccipital by the opisthotic is difficult to ascertain. LANGSTON suggested, on the basis of some suture lines on the braincase of *Lophorhynchon*, that the opisthotic formed a short process which overlapped the base of the paroccipital process.

It therefore appears the exoccipitals and opisthotics fuse early in the evolutionary lineage hypsilopho-

dontid — iguanodontid — hadrosaur, so that both contribute to the formation of the paroccipital process. Of the two bones, the exoccipital seems, especially in the more advanced forms to play an increasing role in the formation of the paroccipital process, apparently at the expense of the opisthotic. The expansion of the exoccipitals is reflected in their excluding the supraoccipital from the foramen magnum in the later ornithopods (*Iguanodon*, *Tenontosaurus*, *Ouranosaurus*) and hadrosaurs.

The reasons for this rearrangement of the occipital bones may be, in part, a manifestation of the functional changes occurring in the crania of these forms. In the more primitive members, typified by *Hypsilophodon*, the skull is small and compact, and yet light and kinetic. The principal changes from this skull type to that seen in the most advanced ornithopods are an increase in size and specializations toward more efficient mastication. The latter, naturally one of the main formative influences on cranial development, has caused various changes in skull architecture, including an increase in snout length, an elaboration of the dentition, an increase in the depth of the skull and a trend toward loss of kinesis.

Initially, the supraoccipital appears to have occupied a key position in the occiput of primitive ornithischians (GALTON, 1974 : *Hypsilophodon*) being involved in a metakinetic joint with the parietal. However, as a result of progressive adaptations to withstand the stresses caused by mastication, this primitive kinetic joint was stabilised. A direct result of this change appears to be the hypertrophy of the exoccipitals, which ultimately isolate the supraoccipital from the foramen magnum. The exoccipitals, having assumed an anchoring role in the hind end of the skull, combine with the opisthotics to support the paroccipital process. The resulting stout occipital plate thus provides a rigid framework to support the remainder of the skull.

On the dorsal part of the occipital plate there is a pair of small foramina, one on either side of the supraoccipital (fig. 4 B, vcd) which run forward and open out into the temporal region of the skull adjacent to the braincase (fig. 9, vcd); these are the *post-temporal foramina*. Each foramen runs along a channel floored by the supraoccipital and by the opisthotic anteriorly and appears to be roofed by the squamosal.

The post-temporal foramen (fenestra or fossa of others) represents an aperture in the occiput through which passes the *vena capitis dorsalis*, a vessel which drains the muscles of the spino-occipital region in modern sauropsids (COX, 1959). After passing through the occipital plate, the *vena capitis dorsalis* emerges anteriorly in the temporal region of the skull, where it then enters the braincase through a cleft (paf — the parietal fissure) and drains into the transverse sinus of the *vena cerebri media*. Details of the cranial circulatory system of *Iguanodon* are to be described elsewhere.

POSTCRANIAL.

Natural posture of *I. bernissartensis* and *I. mantelli*.

The first attempts to produce a skeletal restoration of *Iguanodon* were made using very imperfect material. The first known restoration is that made by GIDEON MANTELL c. 1835 (fig. 74). This sketch was based on the partial skeleton of the « Maidstone *Iguanodon* » discovered in 1835, from which several of the bones can be identified. It was given the proportions of an iguanid lizard since it was believed to have been an extinct species of this family. By a simple process of arithmetical scaling of comparable limb bones and teeth it was estimated that *Iguanodon* had a body length in excess of 100 feet.

ence of a sacrum of five fused vertebrae and upright limbs. As OWEN pointed out, all these features are known in the large pachydermal mammals; he therefore proposed that the dinosaurs were a group of reptiles from the Mesozoic which were equivalent in form to the Cenozoic pachydermal mammals. Indications that all was not well with OWEN's dinosaur restorations resulted from new discoveries of dinosaurs from North America. LEIDY (1858) described a new dinosaur (*Hadrosaurus*) from the Cretaceous marls of New Jersey, which, because of the structure of its teeth, was clearly allied to *Iguanodon*. Fortunately, both fore and hind limbs of the new dinosaur were well-preserved and revealed a pronounced difference in their respective lengths. LEIDY therefore proposed that *Hadrosaurus*

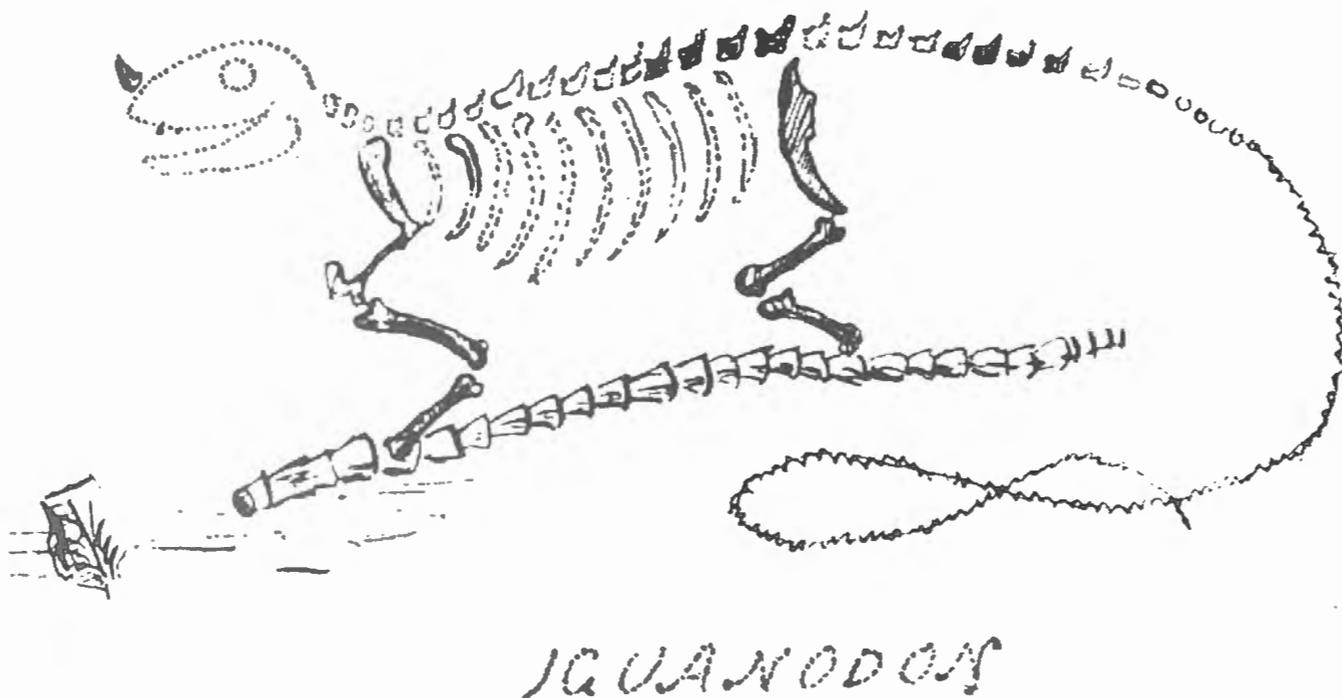


FIG. 74. — A reconstruction of *Iguanodon* made by Gideon MANTELL (circa 1835).
(By permission of the Trustees of the British Museum (Nat. Hist.))

Almost two decades later, in 1854, a new restoration of *Iguanodon* was attempted by Richard OWEN; this formed the basis for life-sized reconstructions of *Iguanodon* by Waterhouse Hawkins for the Crystal Palace site for the Great Exhibition in 1854. The new restoration bore very little resemblance to MANTELL's giant lizard, showing instead a strong similarity to a Rhinoceros, complete with nasal horn (CASIER, 1960: pl. XXII). The reason for this dramatic change in form, even though no new fossil specimens had been found, was the result of detailed anatomical studies on *Iguanodon* and similarly constructed large fossil reptiles *Megalosaurus* (BUCKLAND, 1824) and *Hylaeosaurus* (MANTELL, 1833). In 1841, OWEN published a lengthy report on British fossil reptiles, in which he created a new Suborder, the Dinosauria, for these three reptiles which were characterised by their large size, the pres-

must have been more closely similar in form to a Kangaroo than to a quadrupedal pachyderm as had been suggested for *Iguanodon*.

It was not until 1878, when the first complete skeletons of *Iguanodon* were discovered in Bernissart, that more realised attempts could be made to reconstruct this dinosaur; these skeletons revealed that LEIDY's findings indeed applied to *Iguanodon*. The task of description and reconstruction of the Bernissart dinosaurs eventually devolved to Louis DOLLO and Louis DE PAUW in 1882. The eventual reconstructions of the various *Iguanodon* skeletons (DOLLO, 1883a; 1887a; DE PAUW, 1902, etc.) were certainly influenced by two factors; LEIDY's (1858) and COPE's (1866) demonstration of the affinity of structure of the pelvis and hindlimb of dinosaurs and birds. It is therefore no surprise to find that DOLLO and DE PAUW used the

skeletons of an Emu and a Wallaby for guidance when restoring the very first skeleton of *I. bernissartensis* (see DE PAUW, 1902 : pl. I; CASIER, 1960 : pl. V). The resulting skeletal reconstruction not unnaturally bears a noticeable resemblance to the resting pose of a Kangaroo (fig. 75).

The DOLLO - DE PAUW type of reconstruction has been generally accepted and has appeared in numerous publications since the 1880's. The only serious attempt to modify the posture of *Iguanodon* was made by HEILMANN (1926 : fig. 111); this is a flesh restoration of two *Iguanodon* running at speed, with the body held forward and the tail raised from the ground; the overall

Quite recently, GALTON (1970) reassessed the evidence bearing on the probable posture of hadrosaurs. As a result, he was able to demonstrate that hadrosaurs, most ornithopods and many theropods normally held their vertebral columns more or less horizontal during bipedal running. The principal evidence for this proposal was :

« The ramrod straight posterior dorsal, sacral and anterior caudal vertebrae, the slender pubic peduncle and the shallow curve of the acetabulum show that the straight part of the vertebral column was held more or less horizontally ».

(GALTON, 1970 : 465)

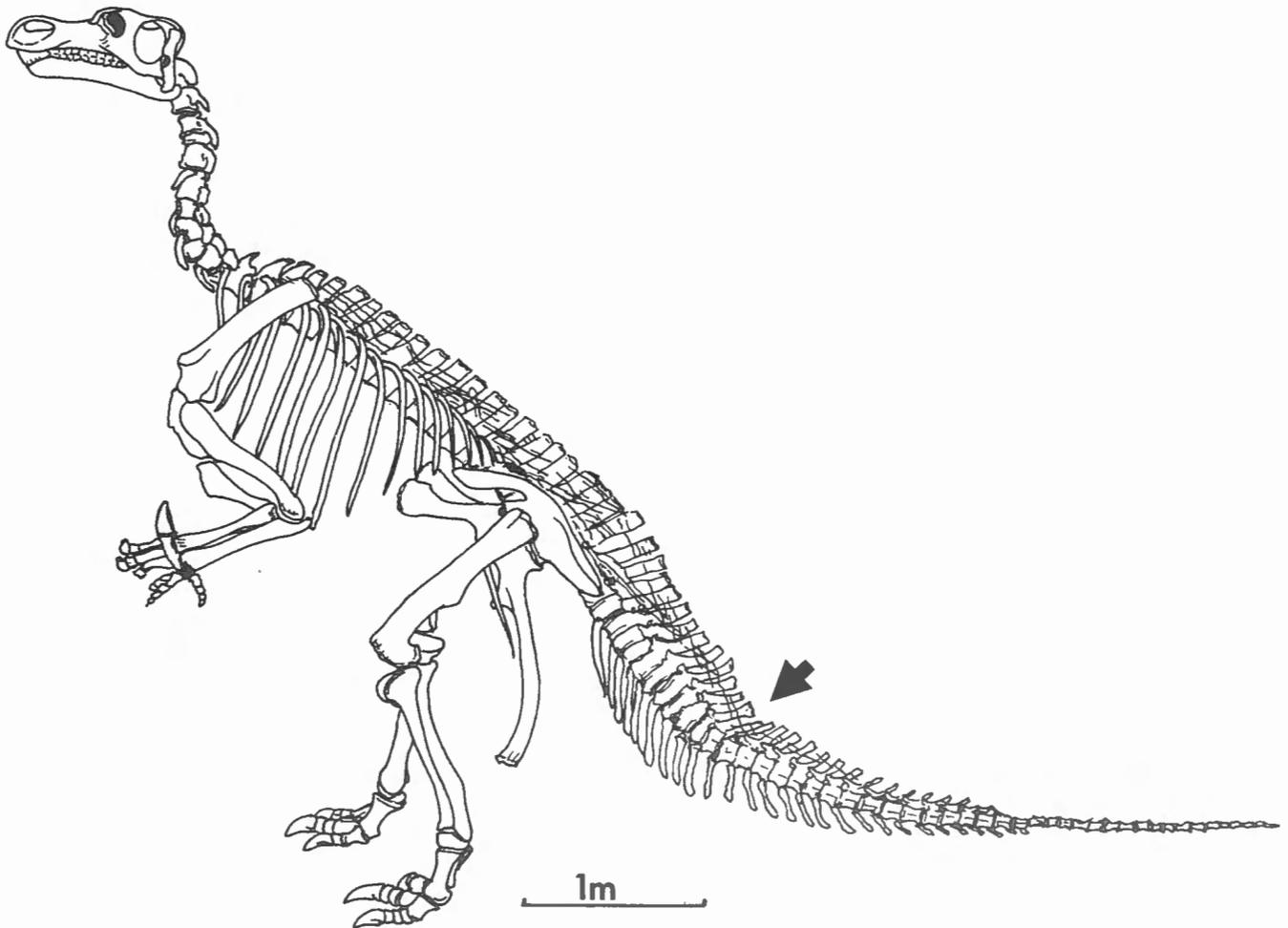


FIG. 75. — A reconstruction of *Iguanodon bernissartensis*. Redrawn from DOLLO (1882a).

effect of this restoration is decidedly more life-like than the DOLLO - DE PAUW version, although it does give an unrealistically rapid gait to an animal weighing as much as a large elephant. However, in the light of a previous paper by DOLLO (1923), HEILMANN revised his 1926 restoration to that seen in HEILMANN (1928) which returned *Iguanodon* to the DOLLO - DE PAUW posture, with an even more accentuated upright stance; this accorded with DOLLO's views that *Iguanodon* was an high arboreal browser which filled the ecological niche occupied, in the present day, by the Giraffe.

Thus GALTON restored the hadrosaur *Anatosaurus* « in a hurry » in a posture remarkably similar to that intuitively produced by HEILMANN (1926) for *Iguanodon*.

There are several observations which suggest that the posture of *Iguanodon* described by DOLLO (fig. 75) is incorrect.

a) The proximal portion of the tail of *I. bernissartensis* has been broken (fig. 75, arrowed) in order to produce the « Kangaroo-like » curvature of the tail. This has also happened in the specimen of *I. mantelli* from Bernissart (IRSNB. 1551) but is less obvious;

BERNISSARTENSIS FROM THE LOWER CRETACEOUS OF BERNISSART (BELGIUM)

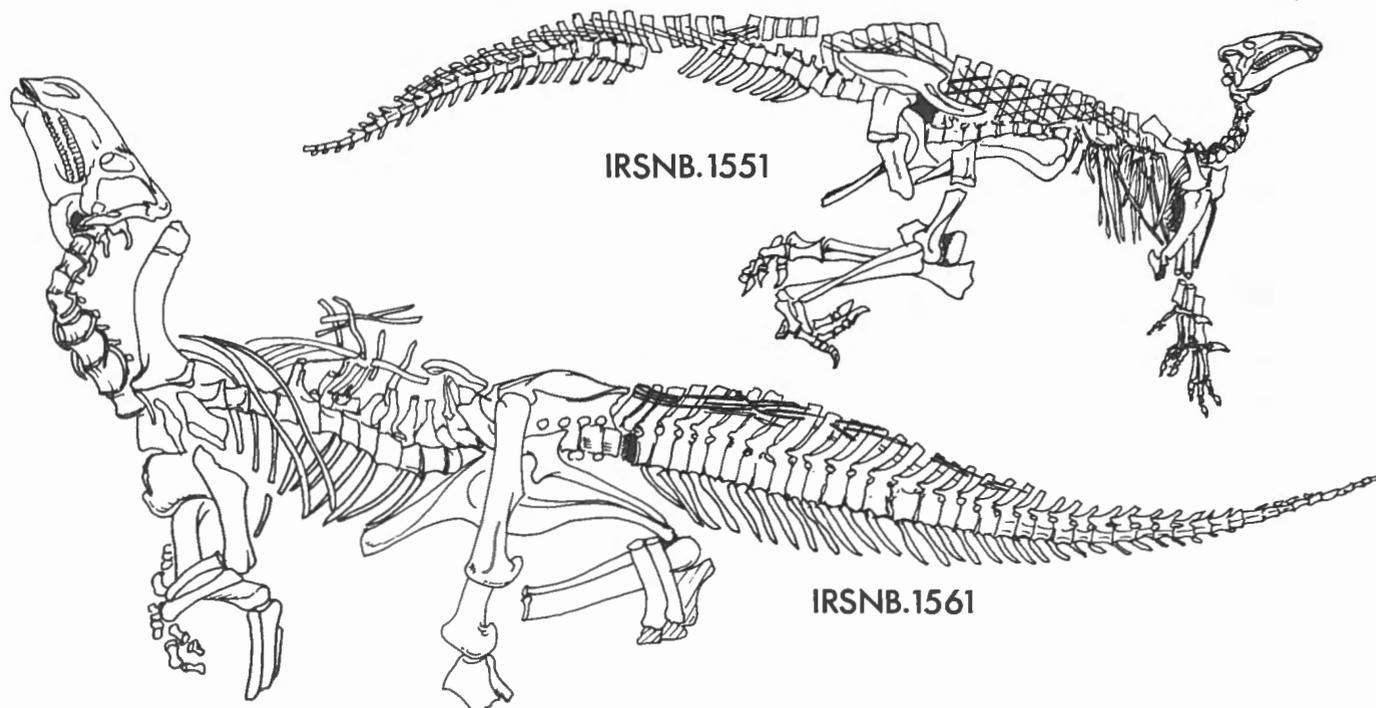


FIG. 76. — *Iguanodon bernissartensis*. (IRSNB. 1561), and *I. mantelli* (IRSNB. 1551) as preserved *in situ*.
Redrawn from original archive material. Originals by G. LAVALETTE.

the tail has been broken in several places, thus disguising the general downward curvature of the articulated sections between the breaks. In addition, the tail as preserved is shorter and the legs have been artificially elongated. As can be seen from drawings of these species made as they were originally preserved (fig. 76), the tail was normally held straight — as GALTON (1970) showed in hadrosaurs — and appears to have been held in this position by the lattice of ossified tendons along the neural spines.

b) The swan-like curvature of the neck has also been artificially produced. This is especially obvious in the skeleton of *I. mantelli*, where the atlas and occipital condyle are completely disarticulated. The normal curvature of the neck was such that it continued on from the dorsal series as a smooth, shallow sigmoid curve. In particular, the skull was quite firmly articulated to the atlas vertebra by a pair of small pro-atlases above the neural canal, which were bound to the exoccipitals thus preventing dorso-ventral flexure of the head at the atlanto-occipital joint.

c) A less obvious feature is related to the construction of the vertebral column on either side of the sacrum. The vertebral centra can be seen to be progressively broader and taller as they approach the sacrum from either side, and their neural spines become progressively broader and taller as they approach the sacrum from either side and their neural spines become progressively taller. There is also a gradual upward curve to the posterior dorsal and anterior caudal centra which seems to be an adaptation to counteract the tendency of the vertebral column to sag. Similarly the ossified tendons have their greatest concentration over the sacrum and adjacent dorsal and sacral vertebrae,

while their number diminishes along the dorsal and caudal series.

Assessing the significance of these factors, there seems to be strong evidence that the vertebral column of *Iguanodon* was normally held more or less horizontally. Straightening the tail to produce a more natural curvature inevitably lowers the thorax. In this pose, the body tends to become balanced about the pelvis, with the massive tail counterbalancing the thorax and head; thus the head and neck can attain a more natural curvature, with the head held forward and slightly downward. The horizontal posture of the body serves to explain the symmetrical construction of the vertebrae about the sacrum and their upward curvature, in relation to the compressive stresses produced in balancing the body at the hips; also the concentration of the ossified tendons about the sacrum corresponds to the area where tensile stresses would be predicted to be greatest, at the base of the trunk and tail.

However, the structure of the ilium and sacrum do not suggest that the vertebral column was held *exclusively* in an horizontal position as GALTON has claimed (1970 : 471). The pubic peduncle of the ilium (fig. 63 - pu.p) although it appears to be a rather slender process when considered in isolation, was clearly adapted to receive the femoral head and the stresses associated with weight support.

The pubic peduncle is triangular in cross-section (fig. 63, shaded profile). Its base, the acetabular surface (ac) is smooth, slightly concave and faces ventrally and slightly laterally. The external edge of this surface forms a sharp rim to be acetabulum, which separates this surface from the slightly convex dorso-lateral surface of the peduncle. The dorso-medial surface is

very heavily scarred where it receives the massive outer surface of the first sacral rib (fig. 63, sa.r). The combination of broad, cupped acetabular surface, the sharp acetabular margin and the massive supporting first sacral rib, suggest that the pubic peduncle was well able to support the femoral head. Indeed, the articular surface of the pubic peduncle is broader than that of the more posterior and dorsal part of the acetabulum and is perhaps therefore better adapted to receive the femoral head. Incidentally, although GALTON (1970) invokes the slender and therefore weak pubic peduncle of the ilium as one of the principal reasons for hadrosaurs and other ornithopods having a normally horizontal vertebral column, he states on another occasion :

« The slender [pubic] peduncle region is therefore backed by the first sacral rib through which the thrust from the femur is transmitted to the vertebral column... In these dinosaurs, [hysilophodontids and iguanodontids] as was probably the case in all lower Ornithopoda, the first sacral rib performed a key role in strengthening the iliac peduncle ».

(GALTON, 1974 : 123-124)

Therefore in *Iguanodon* and possibly many other ornithopods, the vertebral column was probably normally held at a relatively low angle to the horizontal while walking or running. These animals could also have raised the thorax so that the vertebral column was held at between 40° and 50° to the horizontal with ease, and may have done so when stationary and feeding, or when moving slowly. Contact between the tail and ground would probably have prevented them from assuming a more upright posture.

Forelimb function in *I. bernissartensis* and *I. mantelli*.

From a consideration of the anatomy of the vertebral column and pelvis it has been possible to demonstrate that the normal posture of *Iguanodon* was one in which the vertebral column was held more nearly horizontally. A natural consequence of this type of posture is that the thorax and forelimb are brought closer to the ground. STERNBERG (1965) noted that hadrosaurs had a similar type of posture and this led him to propose that hadrosaurs were habitual quadrupeds. However GALTON (1970) was able to show that hadrosaurs, although they did have an horizontal attitude, were bipedal animals. Of the several reasons proposed by GALTON, the most cogent seem to be the very weakly ossified carpus, the relatively loose articulation between the metacarpals, and the forelimb : hindlimb proportions, despite the fact that the ungual phalanges of digits II and III are flattened and hoof-like (BROWN, 1912).

Despite the general belief that *Iguanodon* was bipedal, the anatomy and function of the forelimb have been thoroughly analysed. The methods used for this

analysis are functional morphology, comparative anatomy, biometry and the tangible evidence left as footprints in trackways. Evidence from the musculature of the pectoral girdle and forelimb is largely equivocal (NORMAN, in prep.) but does not specifically preclude the use of the forelimb as a means of either weight support or locomotion.

Functional morphology of the forelimb.

The *humerus* (fig. 57) is typical of most ornithopods in possessing a broadly expanded proximal end, with an off-set, rounded head. Distally the shaft has a slight sigmoid curvature and the delto-pectoral crest is elongate and thickened. The distal portion of the shaft contracts beyond the delto-pectoral crest and terminates at the expanded distal condyles; these latter are separated by a shallow intercondylar groove. The humerus of *I. bernissartensis* is proportionately more stout than that of *I. mantelli*. None of these characters is particularly characteristic of any specific function, although the more massive humerus of *I. bernissartensis* seems better adapted for weight support.

The *radius* (fig. 58) is a stout rod, expanded at both ends. The *ulna* (fig. 58) by comparison, is appreciably more robust and bears a large olecranon (ol) which provides an area for insertion of *M. triceps*, a powerful extensor of the forearm. This feature might be interpreted as an adaptation for quadrupedality, but it should be noted that crocodylians, although they are obligate quadrupeds, do not possess an olecranon process. The forearm space is relatively small indicating that pronation and supination was rather limited. In *I. mantelli* the forearm space is somewhat larger than in *I. bernissartensis*.

Unlike hadrosaurs in which the *carpus* is reduced to two small ossicles, the carpus of *Iguanodon* is fully ossified. In the larger of the species, *I. bernissartensis*, the ligaments and connective tissue which bound the individual carpal bones are ossified, so that the entire wrist is reinforced (fig. 59 : os. ligs, sp.b). The proximal surface of the wrist is excavated by two elliptical depressions for the distal ends of the radius and ulna (fig. 59 c, ra.f, ul.f). By this means the wrist is held firmly against the forearm and it seems unlikely that any movement occurred at this joint. The distal surface of the wrist is also modified in a rather unusual way in order to anchor the metacarpals of the middle three digits. The facets for metacarpals III and IV consist of shallow concave depressions against which the rounded proximal ends of these metacarpals could freely articulate. However, the facet for metacarpal II consists of a deep fossa in the distal surface of the wrist (fig. 59 a) into which the proximal end of the second metacarpal is slotted. This metacarpal is, as a result, firmly anchored in this socket and its range of movements is severely limited. All three features (the fusion of the wrist, its firm attachment to the fore-

arm and the peculiar fossa for the second metacarpal) are adaptations which can be linked to a weight supporting function. The wrist of *I. mantelli*, although not so well-preserved in the specimens known, is well-ossified and similar in overall form to that of *I. bernissartensis*.

The *digits* show considerable differences in form and this seems to reflect some differentiation for the performance of several quite distinct functions.

The first metacarpal is incorporated into the wrist and is a block-like element on the medial side of the wrist (fig. 59, mc.I). Its articular surface has the form of an elongate cylinder, whose long axis is proximo-distally orientated. As a consequence, the thin, plate-like proximal phalanx and its large conical unguis are able to rotate in a transverse plane across the wrist. This digit can be flexed so that the unguis approaches the palm, but it seems unlikely that it was able to touch the palm in a grasping position; this digit can also be hyperextended slightly.

The second, third and fourth digits can be considered together because their metacarpals were bound firmly together by ligaments to form a tridactyl functional unit. When articulated, the third and fourth metacarpals are subequal and their proximal ends are level with one another. The second metacarpal is shorter than the other two and lies against the third with its proximal end standing proud. In *I. bernissartensis* the proximal phalanx of digit II is short and block-like and lies tightly bound to the side of metacarpal III. The three metacarpals and the proximal phalanx of digit II thus form a rigid rectangular region at the centre of the palm. In *I. mantelli* the proximal phalanx of digit II is more slender, elongate and slightly curved and appears only to have been lightly bound to metacarpal III (fig. 77).

The second and unguis phalanges of digit II have a similar form in both species. The second phalanx is a short twisted bone. Its proximal articular surface is concave dorso-ventrally, and the axis about which it rotates on the proximal phalanx is oblique. The middle portion of the phalanx is slightly waisted and its lateral side is longer than its medial side. The distal articular surface is broad, dorso-ventrally convex and is continued on to the dorsal surface of the shaft. The asymmetry of this phalanx enables this digit to diverge from digit III (fig. 60). The unguis phalanx is large, roughly conical in shape and is strongly twisted inward along its length. Distally, the phalanx tapers gradually to a rounded point and is dorso-ventrally compressed. The twisting of this phalanx has resulted in the partial obliteration of the lateral claw groove and its supporting rim of bone. This asymmetry of the unguis phalanx is very similar to that seen in the lateral unguis of the pes and appears to reflect the stresses acting on these phalanges, which are splayed to form a stable weight-supporting structure.

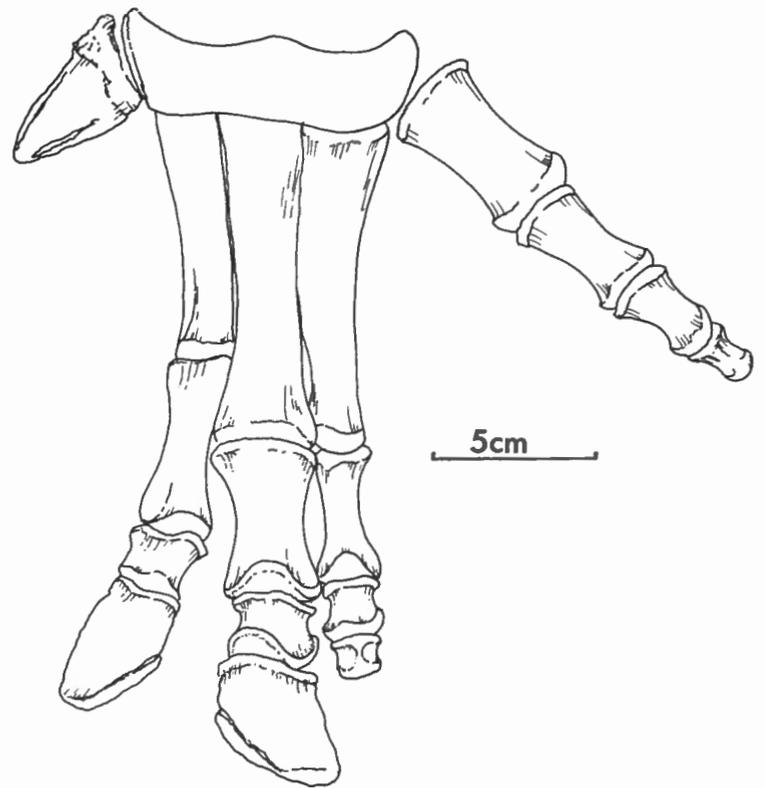


FIG. 77. — *Iguanodon mantelli*. The articulated left manus, based on BMNH. R. 5764.

The proximal phalanx of digit III is stout, symmetrical and block-shaped. Its proximal end is expanded and forms a broad, concave articular surface; it is slightly waisted before re-expanding to produce the distal articular surface which has a shallow intercondylar groove, is strongly convex dorso-ventrally and extends on to the dorsal surface. There are indications that a powerful flexor tendon inserted on to the ventral surface. The second phalanx is proximo-distally compressed and broad, with a dorso-ventrally concave proximal surface and a convex distal surface. In *I. mantelli* (fig. 77) this phalanx is rather more obviously asymmetric than in the large species; its medial side is considerably thicker than the lateral side, and the distal articular surface is far better developed medially than laterally and extends on to the dorsal surface of the phalanx. The unguis phalanx is rather broad and squat compared with that of digit II. Unlike the latter, this unguis is somewhat twisted laterally and the medial nail groove is correspondingly well-developed (figs. 60, 77).

The fourth digit lacks an unguis phalanx and is composed of three phalanges in *I. mantelli* and only two in *I. bernissartensis*. The proximal phalanx of both species is rather stout with expanded proximal and distal surfaces. The former is smooth and cup-shaped, while the latter is strongly convex dorso-ventrally. The second phalanx of *I. bernissartensis* (fig. 60) is broad and compressed proximo-distally with a concave proximal surface and a rounded distal surface. In

I. mantelli (fig. 77) the second phalanx of this digit is a small rectangular bone, the articular ends of which are expanded. The third or terminal phalanx is smaller than the second and has a sub-conical form, the apex having been truncated and rounded.

The fifth digit diverges from digit IV. The fifth metacarpal is considerably shorter and more stout than those of digits II - IV and appears slightly twisted along its length. The proximal end is expanded, depressed at its centre and does not bear a very close relationship to the articular surface of carpal V. The surface of carpal V is directed ventro-laterally so that the metacarpal when in articulation is directed obliquely outward, away from the other digits. Distally, the shaft of the metacarpal is waisted and the ventral surface of that of *I. mantelli* is quite scarred for insertion of a flexor tendon. The distal end of this metacarpal is expanded and the articular surface has the form of a low dome; its articular relationships with the proximal phalanx are thus unclear but undoubtedly allowed a very free range of movement.

The proximal phalanx appears to be a smaller version of the metacarpal except that its shaft is not twisted. Its proximal articular surface is depressed and its distal surface is more convex dorso-ventrally than transversely. The ventral surface of the shaft is somewhat flattened compared with the dorsal and lateral surfaces. The second and third phalanges show similar features to the first but are of smaller size. There are four phalanges to this digit in *I. bernissartensis*, the fourth being variable in form, from a thin convexo-concave disc to a small subconical element. There are only three phalanges to this digit in *I. mantelli*. The possible significance of the distinctive morphology of the manus is considered below.

Weight-supporting adaptations of the manus. — As has already been stated, the wrist seems to be constructed so as to resist compression stresses which are produced by weight-support. Similar adaptations are also to be found in digits II - IV.

Firstly, the metacarpals of these digits were bound together by connective tissue; the close correspondence of shape of their adjacent sides and the considerable scarring of these surfaces suggests that these bones were locked together very tightly. This arrangement, whereby the metapodials are tightly bound together, parallels to some extent the adaptations for weight-support seen in the pes. In the latter, the metatarsals have undergone a considerable amount of re-shaping so that the adjacent surfaces of their proximal halves fit very closely and are prominently scarred by ligaments. The implication therefore is that metacarpals II - IV are adapted for weight-support of a digitigrade or an unguligrade manus. However, the analogy with the pes should not be taken too far. The structure of the pes has evolved as an exclusively weight-supporting structure, thus the metatarsals diverge toward their

distal ends producing a stable, splayed digital arrangement. In the manus, the weight-supporting adaptations are superimposed on an originally grasping type of manus (see *Hypsilophodon* GALTON, 1974 : 135); its construction has therefore been secondarily modified. Thus the mobility of the meso/metapodial joint has been greatly restricted by metacarpal II locking into a fossa in the carpus, this prevents the manus from being used in a plantigrade manner and ensures that the metacarpals contribute to the effective length of the forelimb. Similarly, the metacarpals are bound together along their entire lengths, unlike the metatarsals whose distally splayed form ensures that the digits diverge to form a stable, symmetrical foot. In the manus the digits are also splayed, but this has been achieved by modifications to the phalanges. Metacarpal II is also considerably shorter than either III or IV; this would be an undesirable feature in a supposedly symmetrical, supporting manus, but appears to have been compensated for in *I. bernissartensis* by its short proximal phalanx which was bound quite firmly to the side of the distal end of metacarpal III. This arrangement produces a firm rectangular palm to the manus against which the phalanges articulate. Finally, as with the metatarsals, the metacarpals show another feature which is essential if the manus is to be used, as proposed here, for weight-support; this is the continuation of the phalangeal articular surfaces on to the dorsal surface of the shaft, thereby allowing the phalanges to be hyper-extended.

Concerning the phalanges, there are several general points which indicate that these could have formed weight-bearing structures. All the phalanges are moderately short, squat elements and would appear to be better adapted for weight support, unlike the more slender elongate phalanges normally associated with a grasping or prehensile manus. Secondly and perhaps more importantly, the phalanges of all these digits can be hyper-extended, a function which is compatible with the production of a stable digitigrade foot. Thirdly, the large terminal (ungual) phalanges of digits II and III are dorso-ventrally flattened, twisted and bear large asymmetric claw grooves. This combination of characters again suggests that these digits were used for weight-support rather than for grasping. In the grasping type of manus, one of the most characteristic features of the ungual phalanges is that they are narrow and strongly arched, see for example *Coelurus* (*Ornitholestes*) (OSBORN, 1917) or *Heterodontosaurus* (SANTA-LUCA, *et al.*, 1976).

If the phalanges of digits II - IV of the manus are articulated together in a hyper-extended position, they form a reasonably stable weight-bearing structure in both species (figs. 78, 79). In *I. bernissartensis* (fig. 78) the proximal phalanx of digit II has its lateral side closely appressed to the distal end of metacarpal III; however its distal articular surface is twisted



FIG. 78. — *Iguanodon bernissartensis*. (IRSNB. 1558). The articulated left manus in an hyperextended (weight-bearing) position. Redrawn from a photograph.

medially, and the more distal phalanges therefore diverge from digit III when fully extended. The second phalanx is wedge-shaped and continues this trend, which culminates in the large, curved unguis phalanx. The whole digit is thus distinctly hooked inward (medially) when fully extended. A similar feature is seen in the lateral digits of the pes and represents an adaptation to improve stability and traction in the pes. Digit III is rather less asymmetric than the second: the proximal and second phalanges are larger and more symmetrical than those of digit II, while the unguis phalanx is considerably shorter, broader and more dorso-ventrally flattened than that of digit II (figs. 60, 78). When hyper-extended, this digit curves slightly laterally toward its distal end and thus diverges from digit II. The fourth digit, although considerably shorter than the previous two and lacking a claw-bearing unguis phalanx, also appears to have had a weight-supporting function; its proximal phalanx is large, robust and

block-like, the distal articular surface of its metacarpal faces obliquely outward (laterally). Thus this phalanx diverges from digit III. The terminal phalanx consists of a proximo-distally compressed bone with its distal surface broad and rounded.

The manus of *I. mantelli* (fig. 77) is notably more gracile than that of *I. bernissartensis* and there is a slight difference in the structure of digit II; its proximal phalanx is long, slender and curved by comparison to that of *I. bernissartensis* and, because of the oblique form of its proximal end, this phalanx diverges markedly from metacarpal III in the fully extended position (fig. 79). Digit IV is proportionately more slender than that of *I. bernissartensis* and has an additional phalanx.

Functionally, the middle three digits of the manus of *I. bernissartensis* and *I. mantelli* were capable of being used for weight support and locomotion. The more robust construction of these digits in *I. bernissartensis* probably reflects not only the greater size of



FIG. 79. — *Iguanodon mantelli*. (Based on BMNH. R. 5764)
The left manus in a weight-bearing position.

this species, but also a difference in the mode of life of these two species.

From a purely functional point of view, the middle three digits of the manus might have been expected to form a symmetrical structure similar to that seen in the pes; however this was never possible. In the ornithopods from which *Iguanodon* evolved, digits IV and V appear to have early become reduced. Gradual reduction of these digits with eventual loss of their ungual phalanges can be seen in the Triassic *Heterodontosaurus* (SANTA-LUCA *et al.*, 1976) as well as the Jurassic *Camptosaurus* (GILMORE, 1909: fig. 28) and the generalised Cretaceous ornithopod *Hypsilophodon* (GALTON, 1974: fig. 41). The asymmetry of the manus of *Iguanodon* is thus a very appropriate example illustrating DOLLO'S LAW.

Grasping adaptations of the manus. — It would appear to be rather unlikely that digits II - IV were used for grasping objects in any precise manner (fig. 80). There are two particular features of these digits which are not consistent with a grasping ability: firstly, the digits diverge, even when fully flexed (fig. 80) so that opposition was impossible and secondly, digits II and III possess broad, flattened, hoof-like unguals, the massive horny claws of which would obviously have been ill-equipped for grasping objects. Digit IV of *I. bernissartensis* is obviously too short to have had any practical use for grasping, although it is possible that in *I. mantelli*, where this digit is more slender, some limited grasping occurred.

Of the remaining digits, V is the one most obviously adapted for grasping (fig. 80). Its metacarpal is relatively short and in fact has proportions similar to those of the proximal phalanges of digits II - IV. It also has an extremely wide potential range of movements. Its proximal surface is a shallow depression and articulates against the rounded surface of carpal V; it is very difficult therefore to set limits on the mobility at this joint. Similarly the distal end of metacarpal V is merely a convex surface on which the proximal phalanx sits. The remaining phalanges (three in *I. bernissartensis*, two in *I. mantelli*) appear to articulate more or less conventionally in a dorso-ventral plane although considerable lateral rotation was undoubtedly possible. The apparent axial twisting of this metacarpal which was described earlier appears to reflect the ability of this digit to be opposed to the palm region of the manus. The length of this digit, the number of moveable segments (four or five) and the great degree of freedom of the joints at its base, all suggest that it was suited for grasping. Whether it was used merely as a single prehensile organ or was capable of being opposed to the other digits (I or IV) is uncertain.



FIG. 80. — *Iguanodon bernissartensis*. (IRSNB. 1558).
The left manus in a flexed (grasping) position.

The function of the pollex. — The function of the characteristic pollex of *Iguanodon* has long remained obscure. Initially, it was thought to represent the core of a horn which had been on the nose of the animal (see fig. 74 - MANTELL, 1827). Much later, OWEN was able to demonstrate that the supposed horn core was most probably an ungual phalanx, and suggested that it belonged to the pes (OWEN, 1858) and still later suggested that it represented a radial spine which bore a superficial resemblance to the radial spine used as a mating grapple by anuran Amphibia (OWEN, 1872). Consequently, OWEN suggested that this radial spine served a similar function in *Iguanodon*, either serving as a grapple for mating, or alternatively as a

defensive weapon against the carnivorous megalosaurs. DOLLO (1882) was the first to demonstrate that the enigmatic bone described previously was the ungual phalanx of the pollex. LYDEKKER shortly afterwards (1890) described the first evidence which suggested the use of the pollex spur. He described a newly discovered scapula (BMNH. R. 996) from the Wadhurst day, which bore a large lesion on its external surface. This, it was suggested, represented a partially healed wound caused by a blow from the ungual of the pollex. It seemed unlikely that such a wound would have been the result of mating! The likelihood was, therefore, that the wound was the result of intraspecific combat between male *Iguanodon*.

Whatever the actual cause of the lesion on the scapula, the possibility that the pollex was used as a defensive weapon is the explanation which most readily accords with the known facts. The pollex ungual and its proximal phalanx are intimately associated; the latter forms a plate-like disc which was apparently bound by ligaments to the proximal surface of the ungual. The single moveable joint in the pollex occurs between the proximal phalanx and the stout metacarpal, and the movement which is possible appears to be mostly limited, by the shape of the metacarpal, to transverse rotation across the wrist. When fully flexed, the pollex would have occupied a position almost at right angles to the palm and perhaps in a position where it could have opposed the fully flexed digit V (fig. 80), although whether these two could have been used together for grasping is uncertain. In *I. mantelli*, the ungual phalanx of the pollex is relatively small and very little curved along its length, but it possesses a well developed claw groove (fig. 77). The pollex was, therefore, almost certainly provided with a large and, judging by the shape of the ungual, spine-like slightly curved claw. While this might have been used simply as a hook for moving objects, it seems more probable that it would have been rather better used as a weapon at close quarters. The reduction of the number of joints to one would have improved the strength of the pollex for slashing movements, while the limited mobility would have enabled the claw to be flexed and repositioned. The only other possibility would seem to be that the pollex was used as a device for obtaining food, either as a means of stripping foliage from branches or as a digging tool for excavating roots and rhizomes of *Equisetum* sp., upon which the species might have fed.

One point of possible significance to the consideration of the probable function of the pollex, is the condition in *I. bernissartensis*. In this species, the ungual phalanx of the pollex is in proportion considerably larger than that in *I. mantelli*, and forms an enormous, slightly curved, pointed conical spur, 200 mm or more long. Since this also carried a horny claw, the total length of the ungual phalanx and claw alone may

have been as much as 300mm. This relatively large sickle-shaped claw would have been of little use other than as a defensive weapon; it would obviously have been too large and clumsy to have been used for grasping. The great difference in size of the pollex ungual phalanx in these two species needs an explanation; the only adequate explanation appears to be also in terms of a defensive function for the pollex.

As will be shown, there is good reason to suppose that *I. mantelli* represents a small, moderately lightly built species, capable of spending the majority of its time walking and running bipedally. *I. bernissartensis*, on the other hand, represents a large, robustly constructed species, which most probably, as a result of its size, spent most of its time (at least when adult) walking quadrupedally. Assuming that these proposals are correct, then the probable method of defence against the large carnivorous megalosaurs may have differed in these two species. The smaller, more agile, species could have fled from, rather than fought, these predators; the larger more cumbersome species however, may have been less well able to flee from the presumably moderately agile carnososaurs, and therefore had to rely on defence. Thus theoretically at least, the smaller agile species did not need well-developed pollex spines as greatly as the larger, less agile, species, perhaps accounting in terms of function and natural selection for the hypertrophy of the pollex in *I. bernissartensis*.

Conclusion. — The proximal elements of the forelimbs (humerus, radius and ulna) provide of unequivocal evidence concerning the use of the forelimb either as a weight supporting or as a prehensile organ. The carpus is well ossified and its individual bones are firmly bound together by ligaments, which become ossified in *I. bernissartensis*; the carpus is firmly held against the forearm by ligaments, which prevented any excessive movement. All these features suggest that the carpus was able to support weight and did not provide the very mobile structure which is usually associated with a prehensile (grasping) manus. The digits of the manus show differentiation into three functional units: *digit I*, which is restricted in its mobility and was probably a defensive weapon; *digits II - IV*, which seem to have provided a moderately stable weight supporting structure, comparable in some of its characters with the digits of the pes — *digit IV* may possibly have had a grasping function in *I. mantelli*; *digit V* was most probably the only truly prehensile digit, since it was capable of a wide range of movements, and has several joints which facilitate strong curvature of this digit. The manus of *I. mantelli* and *I. bernissartensis* show different degrees of specialisation; these differences can be attributed to the proposed differences in mode of life of the two species.

Functional morphology of the pectoral girdle.

The *scapula* is well-developed in both species of *Iguanodon*, although it is somewhat straighter and stouter in *I. bernissartensis*. Also, the glenoid and its thick dorsal buttress are very well formed and constitute part of a deep socket to receive the head of the humerus (fig. 52 B, gl). The ventral edge of the scapula is thickened and is sutured to the coracoid and, although this junction remains unfused, it was nevertheless a very strong suture. The postero-dorsal edge of the coracoid is excavated to form the remainder of the glenoid (fig. 53 B). There are therefore no obvious features which suggest that these elements were unable to support the forelimb in a quadrupedal stance, unless it be perhaps the lack of fusion of scapula and coracoid to produce the scapulo-coracoid characteristic of obligate quadrupedal ornithischians. However, the scapula/coracoid suture is well-developed and thickened transversely to increase its strength, and the glenoid is deep and well buttressed, suggesting an adaptation toward receiving the vertical thrust from the head of the humerus.

In the area occupied by the sternal cartilage are the paired *sternal bones*. These are found just posterior to the coracoid on each side of the ventral midline. They are hatchet-shaped bones, the handle of the hatchet directed postero-laterally, and the blades separated by a short distance across the midline. These bones are well-developed in bipedal and quadrupedal ornithischians alike; they presumably helped to brace the sternal cartilage and supported the sternal ribs, and do not seem particularly good indicators of bipedality or quadrupedality. However, in *I. bernissartensis* alone, there is frequently found a large irregular intersternal ossification in the area of the sternum between the coracoids and sternal bones (figs. 55, 56). Despite the rather irregular appearance of this « ossification », it has at least one common character, and that is the presence of grooves along its lateral edges; these can be fitted against the medial edges of the coracoids forming an arrangement reminiscent of the sterno-coracoid hinge found in lacertilians.

The only immediately obvious explanation of the presence of these « ossification » in the sternal area is one related to the stance and use of the forelimb in the large species, *I. bernissartensis*. The rather irregular appearance of these « ossification » seems to suggest that they have arisen secondarily from within the cartilage of the sternal plate. The circumstances which led to the formation of this structure may have resulted from the prolonged use of the forelimb for locomotion in this species. A consequence of locomotion and weight support in this species was that some stresses would have acted across the ventral surface of the pectoral girdle. This might therefore have led to the deposition of bone salts which would have served to reinforce the cartilage of the sternal plate between the coracoids.

A similar intersternal ossification has been found in the Lower Wealden species *I. fittoni*. One specimen (BMNH. R. 1835) demonstrates a condition in which the « intersternal ossification » has enlarged and caused the fusion of the sternal bones into a rigid plate. The coracoids, however, have not as yet become fused to this sternal plate, but were received by shallow grooves down either side of the plate.

Thus, although the scapula, coracoid and sternal bones provide no unequivocal evidence with regard to the function of the forelimb, the presence of an « intersternal ossification » in *I. bernissartensis* can be tentatively correlated with the consequence of adopting a quadrupedal gait.

Comparative anatomy of the forelimb.

I. mantelli vs. *I. bernissartensis*. — From the preceding analyses it seems that there are a considerable number of differences in the structure and function of the forelimb in these two species. Indeed, it is patently obvious that there is a considerable difference in the relative proportions of the forelimbs of these two species, if the mounted skeletons of these species in the « Cagé Monté » of the Royal Institute of Natural Sciences, Brussels are compared visually. By contrast, the hind limbs of both these species, and numerous other « graviportal » ornithopods, have essentially uniform proportions of their composite elements. To better and more clearly illustrate the difference in proportions of the forelimbs in the two species of *Iguanodon*, comparative measurements of the elements of the forelimb and hindlimb bones have been taken. Those measurements of the hindlimb of *I. bernissartensis* were scaled down so that they corresponded with those of the hindlimb of *I. mantelli* (fig. 81, st.hl) and then the same scaling factor was used to reduce the forelimb of *I. bernissartensis*. The results are illustrated diagrammatically (fig. 81) and show very clearly the differences in proportions of the forelimbs in these two species.

The most immediately obvious difference between these two species is in the relative size of the humerus; this bone is considerably larger in *I. bernissartensis*. From a practical point of view, the difference in relative size of the forelimb in these species implies that *I. bernissartensis* was much better able to use its forelimb for walking and weight support than *I. mantelli*, because it could reach the ground more easily, and also because it would have had a greater stride length. This agrees very closely with all the anatomical features noted in these species, which suggest that the forelimb of *I. bernissartensis* was better adapted for weight support, than it was in *I. mantelli*.

By way of a comparison, the same procedure of scaling down the hindlimb to that of *I. mantelli* was used to compare the proportions of the forelimbs of two ornithopods: *Anatosaurus* and *Tenontosaurus* (fig. 81 — **Anat.** and **T. till** respectively).

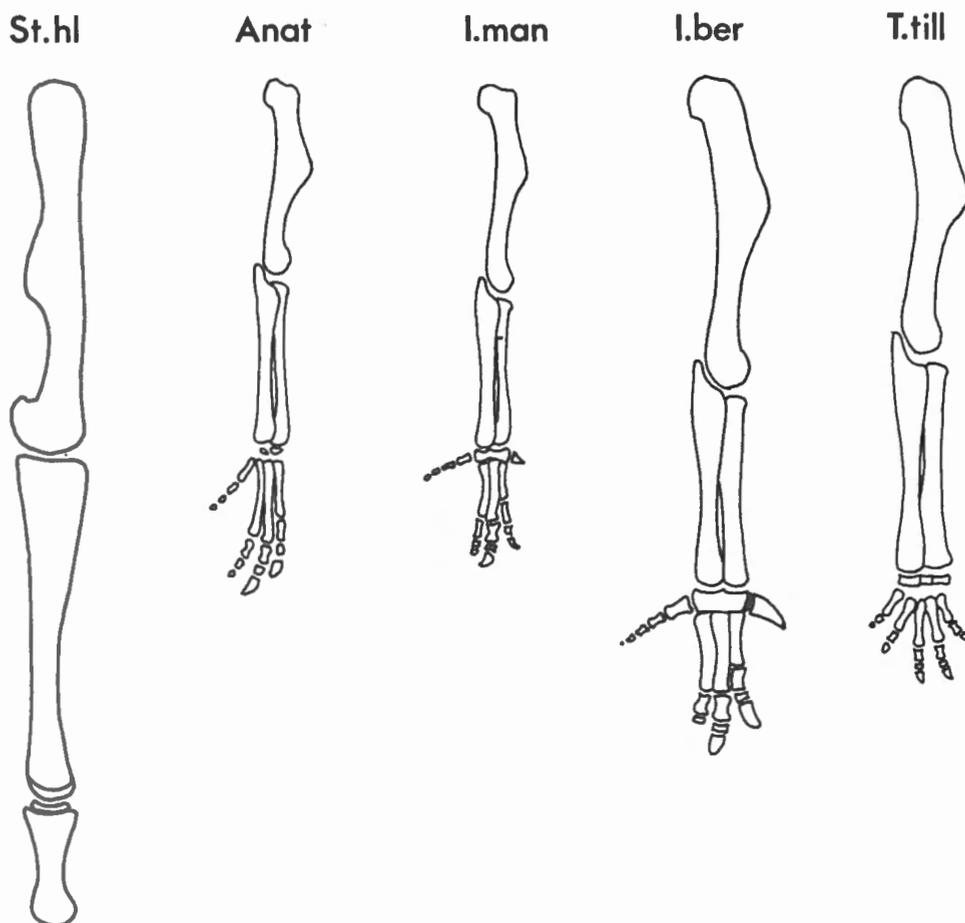


FIG. 81. — Comparison of the relative size and proportions of the forelimbs of selected ornithomorphs.

Anatosaurus. — GALTON (1970) has demonstrated that this species and all other hadrosaurs were bipedal ornithomorphs. Certainly the construction of the manus agrees with this suggestion: the carpus (fig. 81) consists of two small, separate, lozenge-shaped bones, which seem ill-adapted for weight support; similarly the metacarpals are more slender and appear to have been less strongly bound together by ligaments than in *Iguanodon*. The presence of hook-like unguals on digits II and III suggests that the manus might have been of limited use for supporting the animal while stationary or grazing, but this would have been for brief periods only. From the comparative diagrams it is clear that the forelimb proportions of the largely bipedal hadrosaur *Anatosaurus* are almost identical to those of *I. mantelli*. This implies that *I. mantelli* may have had a similar gait to that of hadrosaurs and that the forelimb had a primarily transient role, providing weight support when stationary or while moving slowly. The forelimb of *I. bernissartensis* is much longer and more massive than that of hadrosaurs and cannot be readily compared.

Tenontosaurus. — OSTROM (1970) described the osteology of this new ornithomorph which appears, at least by comparing forelimb and hindlimb proportions, to have been constructed very similarly to *I. bernissartensis* (fig. 81). There are several features in the construction

of the forelimb of this species which suggest that it may have been primarily quadrupedal. As with *I. bernissartensis*, the forelimb is more than two-thirds of the length of the hindlimb and could have reached the ground comparatively easily if the vertebral column was held horizontally. In addition, the manus is well-adapted for a weight supporting, rather than a grasping, function. There were apparently three proximal carpals and at least one, and probably more, distal carpals; unfortunately their structure was not described by OSTROM (1970). However, the manus was very broad and quite short compared with that of *Iguanodon* (loc. cit. pl. 21). The metacarpals are rather short, with expanded ends; the lateral metacarpals are shortest. The first digit has a more conventional form than has that of *Iguanodon*, the proximal phalanx is a rather short block-like bone, with very well developed articular ends which possess intercondylar grooves, as have all the phalanges of digits I - III. The ungual phalanx of this digit is dorso-ventrally flattened, moderately pointed and arched. The whole digit is capable of being hyper-extended and has a slight medial curvature. Digits II and III have a very similar structure to the first and are similarly able to hyper-extend. Digits IV and V are shorter than the previous two and do not bear ungual phalanges, terminating instead with small nubbin-like bones. The fifth digit shows none of the

characters associated with prehensility found in that of *Iguanodon*. The noticeably broad and short manus is best correlated with a weight supporting function, which would also serve to explain the ability of the digits of the manus to be hyper-extended. Although the metacarpals were not as obviously firmly bound together as in *Iguanodon*, nevertheless the manus would still have been an effective weight carrying structure, because the load was shared between all five digits compared to just three in *Iguanodon* and, because the metacarpals were shorter and more stout, consequently better able to bear the loads on the manus than were the longer and more slender metacarpals of *Iguanodon*. I consider it highly probable that the manus of *Tenontosaurus* was used in a manner similar to that of *Camptosaurus dispar*. In the latter species, the manus was of a very similar form to that of *Tenontosaurus* and, in addition, the carpus has been preserved; this was very robustly constructed and well-ossified. The manus and carpus of *Camptosaurus dispar* were illustrated by GILMORE (1909, p. 252, fig. 28) in a typical hyper-extended (weight-bearing) attitude.

Therefore judging by the relative lengths of their forelimbs compared to their hindlimbs, *I. mantelli* is more similar to the habitually bipedal hadrosaurs, while *I. bernissartensis* seems to be more closely comparable to the facultatively bipedal ornithopods like *Camptosaurus* and *Tenontosaurus*.

Hindlimb : forelimb ratios.

Another means of deciding the probable function of the forelimb in *Iguanodon* is the use of fore- and hindlimb lengths in order to produce ratios of their

dimensions which can then be compared either graphically or numerically with those of forms which are less equivocal as regards their gait.

a) **Hindlimb-Forelimb ratio.** — The effective length of the hindlimb and forelimb are considered to be the sum of the lengths of the femur, tibia and metatarsal III, and the humerus, radius and metacarpal III. Since no dinosaurs were unguligrade, it seems reasonable to suppose that the contribution to limb length made by the phalanges was minimal and not significant to these ratios. Among the typically bipedal hadrosaurian dinosaurs, the hindlimb:forelimb ratios are found to average approximately 1.65 (fig. 82; table I) while in the highly cursorial bipedal coeluro-coelurosaurs (GALTON, 1970; *Struthiomimus*) the ratio is far higher: 2.17. By contrast, the corresponding ratios for typically quadrupedal dinosaurs (ankylosaurs, ceratopians and sauropods) are typically less than 1.45 (fig. 82; table I). It is interesting to compare these ratios with those found in the two species of *Iguanodon*. *I. mantelli* has a hindlimb : forelimb ratio of 1.97, which suggests that this species was even more bipedal than hadrosaurs and closer in its limb proportions to some coelurosaurs which were undoubtedly obligate bipeds. *I. bernissartensis* by contrast, has a hindlimb : forelimb ratio of 1.43 and therefore falls within the range of ratios found in typically quadrupedal dinosaurs, in fact from this ratio alone is nearer to quadrupedality than was *Tenontosaurus*. However, this ratio alone is insufficient evidence of bipedality or quadrupedality among dinosaurs. For example the typically quadrupedal stegosaurs retain a great disparity in lengths of forelimb and hindlimb, giving ratios of between 1.4 and 1.7 (table I, fig. 82). This characteristic was com-

TABLE I.

	hindlimb : forelimb	Radius : Humerus	Metacarpal III : Humerus	Index of forelimb proportion
* <i>Lambeosaurus clavinitialis</i> (L.c)	1.65	1.18	0.51	0.60
* <i>Procheneosaurus praeceps</i> (P.p)	1.74	1.05	0.49	0.51
* <i>Saurolophus osborni</i> (S.o)	1.66	1.02	0.54	0.55
<i>Corythosaurus casuarius</i> (C.c)	1.68	1.06	0.44	0.47
* <i>Edmontosaurus regalis</i> (E.r)	1.70	0.92	0.48	0.44
<i>Anatosaurus annectens</i> (A.a)	1.94	0.86	0.44	0.43
* <i>Kritosaurus incurvimanus</i> (K.i)	1.67	0.88	0.36	0.31
<i>Iguanodon mantelli</i> (I.m)	1.97	0.69	0.31	0.21
• <i>Tenontosaurus tilletti</i> (T.t)	1.52	0.75	0.21	0.16
<i>Iguanodon bernissartensis</i> (I.b)	1.43	0.62	0.24	0.15
* <i>Stegosaurus stenops</i> (S.s)	1.71	0.70	0.21	0.15
* <i>Kentrosaurus aethiopicus</i> (K.a)	1.40	0.67	0.19	0.13
* <i>Scolosaurus cutleri</i> (S.c)	1.46	0.61	0.20	0.12
* <i>Nodosaurus</i> sp. (N)	—	0.66	0.26	0.17
* <i>Triceratops elatus</i> (T.e)	1.29	0.50	0.19	0.10
* <i>Apatosaurus</i> (A)... ..	1.35	0.69	0.17	0.12

* Data from GALTON (1970).

• Data from OSTROM (1970).

mented on by GALTON (1970). (It should be noted that more recently Bakker has suggested that stegosaurs may well have been able to raise the front part of their bodies from the ground in order to feed on higher foliage.)

To remove « false-bipeds » such as the stegosaurs, GALTON used another ratio, hindlimb : trunk length;

b) The index of forelimb proportions. — This index is derived by multiplying together the ratios of the lengths, radius : humerus and metacarpal III : humerus (table I). The resultant value represents a numerical indication of the degree to which the distal segments of the limb are shortened or lengthened. The significance of this index relies on the fol-

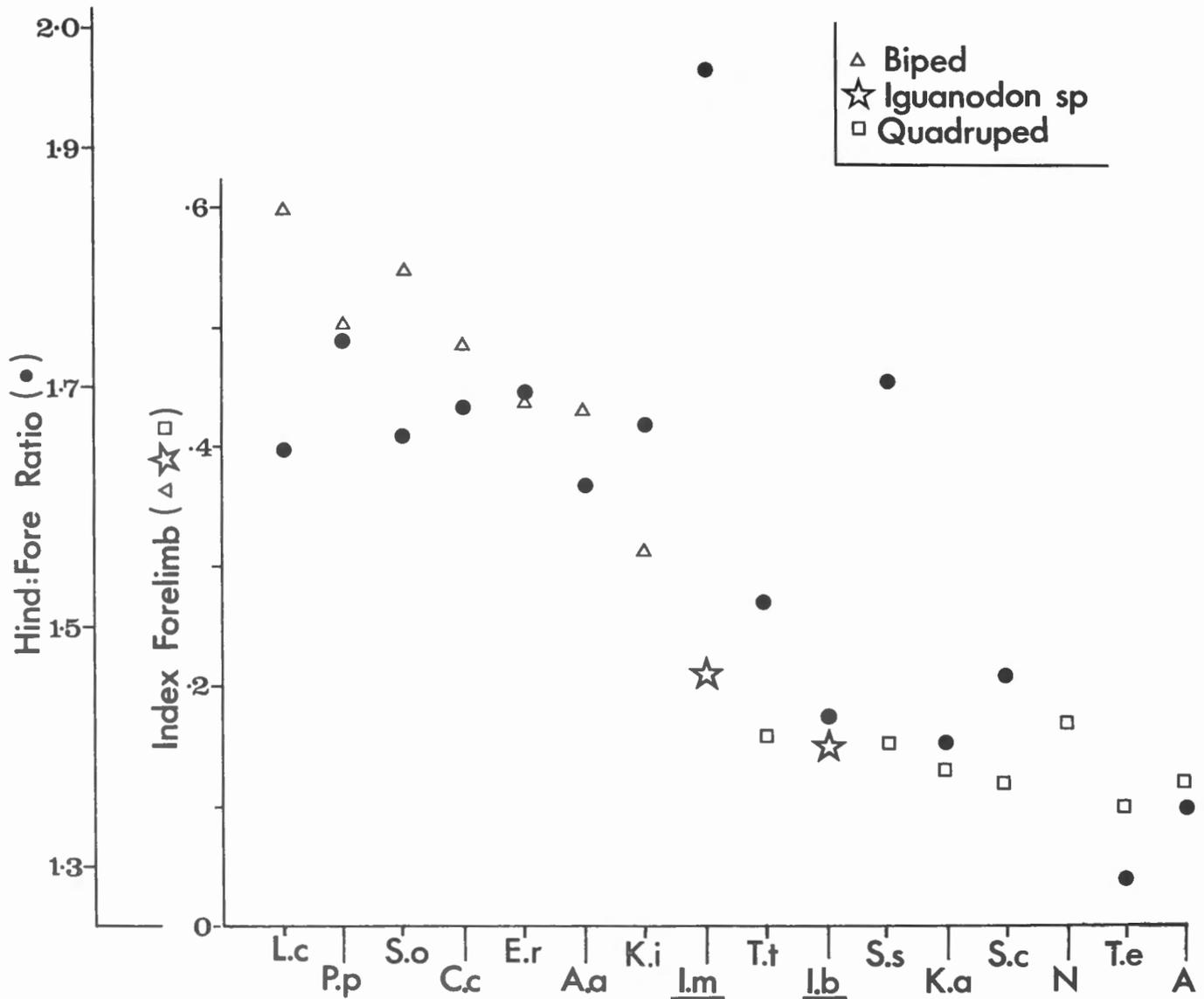


FIG. 82. — Graphical representation of limb proportions in a variety of dinosaurs.

this more clearly separated bipeds from quadrupeds, because bipeds tend to have shorter trunks in proportion to their hindlimbs than do quadrupeds. Another means of removing the « false-bipeds » is here proposed, which relies on the forelimb dimensions alone; this may perhaps be of greater potential use than the hindlimb : trunk ratio, because the latter is frequently impossible or difficult to estimate, due to the imperfect preservation of many fossil species, and the difficulty of correctly positioning the pectoral girdle to obtain a value for trunk length.

lowing supposition : that in dinosaurs, the forelimbs should develop in a predictable fashion which depends on their function. If used as prehensile organs, the distal segments of the limb tend to become more elongate, whereas if the limb is primarily weight supporting, the distal segments tend to become shorter. This is obviously rather simplified as used here, because this index ignores the fact that some of the most characteristic changes which occur in these two modes of life concern the phalanges; these either become long and slender grasping organs or compressed cuboid

elements. Nevertheless, the results do show marked differences for the values of this index between undoubted bipeds (open triangles) and quadrupeds (open squares - fig. 82; table I).

It appears that among the bipedal forms the index has a value greater than 0.3, while in typical quadrupeds (including the stegosaurs) it is less than 0.15. In both species of *Iguanodon*, the values are far closer than would have been expected from the hindlimb : forelimb ratios : 0.21 for *I. mantelli*, which suggests that the proportions of its forelimb are closer to that of a typical quadruped; and 0.15 for *I. bernissartensis*, just within the range of typical quadrupedal forms. *Tenontosaurus*, despite the construction of its manus, has proportions of its forelimb (index = 0.16) which seem marginally less close to quadrupedal forms than is *I. bernissartensis*.

The evidence from preserved trackways.

Numerous impressions of footprints have been found in the Wealden strata, including a few trackways. Several of these have been collected and these were investigated for evidence of the gait of *Iguanodon*. CHARIG and NEWMAN (1962) were able to demonstrate that the tridactyl Wealden footprints were of two quite distinct types. Those which appeared to have rather slender pointed digits, with a characteristically hooked end to the medial digit, were identified as megalosaurian. The second type appeared to have much broader rounded ends to the digits, and these were identified as belonging to *Iguanodon*.

One well-preserved trackway until recently on display in the galleries of the British Museum (Nat. Hist.), (pl. 5), consists of two parallel tracks of footprints. Previously it had been assumed that both of these tracks had been made by a megalosaur. As can be seen in the diagram, one of the tracks has footprints which are typical of those identified by CHARIG and NEWMAN

as megalosaurian. The other trackway is much less well preserved and shows no clear evidence of its affinities. However, imperfect as this trackway is, it is of particular interest because it shows, in addition to the alternate impressions of the hindfeet, a series of smaller oval impressions which are found parallel to, and on either side of, the hind-foot prints. These, it was previously supposed, were caused by a megalosaur, occasionally dragging its forelimbs along the ground. However, in the light of previous findings, it seems much more probable that these impressions were made by the fore-feet of an *Iguanodon* which was walking quadrupedally. A similar, though less extensive trackway of *Iguanodon* is displayed at the Glasgow Museum. The impressions of the hind-feet are far more clearly preserved than in the former trackway and they can be identified as typical of *Iguanodon*. In addition, a similar series of smaller forelimb impressions are preserved; these support the interpretation of the first trackway (Dr. W.D.I. ROLFE, pers. comm.).

Summary : probable function of the forelimb in two species of *Iguanodon*.

The results from the several methods used in an attempt to solve this problem had been surprisingly complementary, and enable the probable function of the forelimb to be described with some confidence.

I. mantelli.

This species has a gracile type of skeletal construction, at least when compared with *I. bernissartensis*. The morphology of the manus indicates that it could have performed at least three quite distinct functions, using specialised groups of digits. These functions were : defence against predators, using the ungual spur on digit I; for grasping objects, using digit V and perhaps also digit IV; and locomotion, using digits II, III and IV. Comparisons with the manus of *I. bernis-*

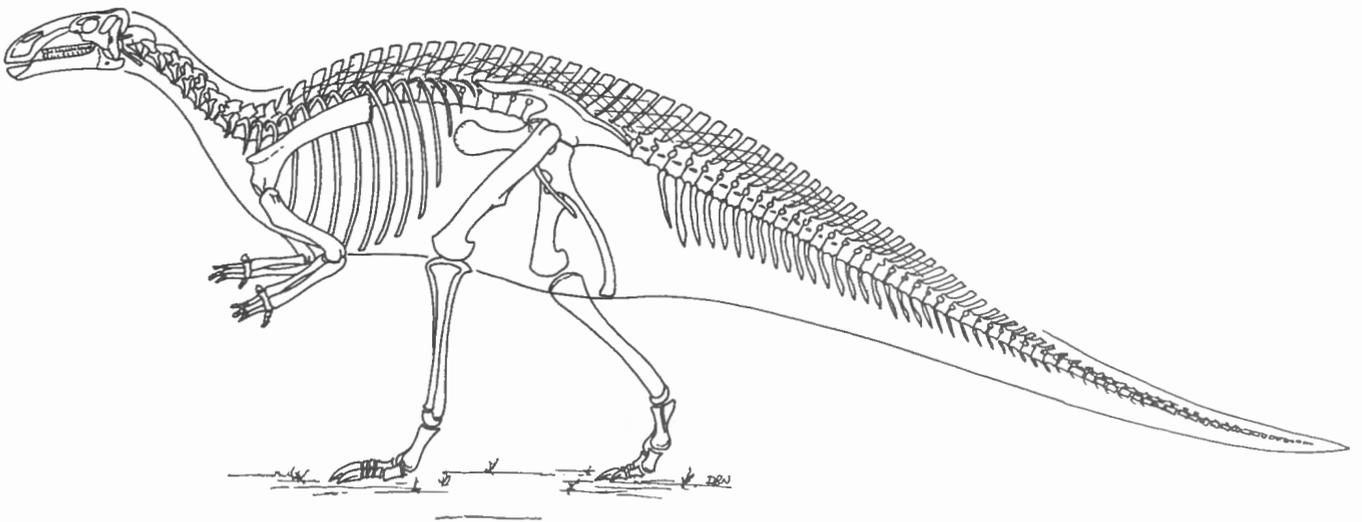


FIG. 83. — *I. mantelli*. An attempt at a complete skeletal restoration in a normal walking pose.

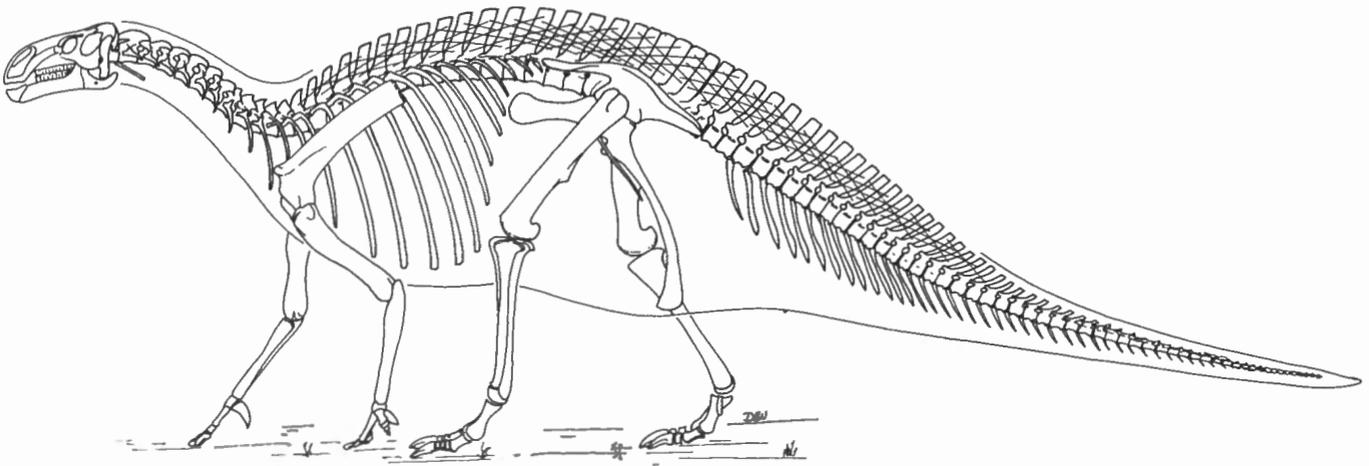


FIG. 84. — *I. bernissartensis*. An attempt at a complete skeletal restoration in normal walking pose.

sartensis showed that the adaptations for weight support were less well-developed than in the latter species. Comparisons of the structure and proportions of the forelimb of this species with *Anatosaurus* and *Tenontosaurus* suggest that it was more similar to the hadrosaurian forelimb; this was confirmed by comparing forelimb : hindlimb ratios of this species with various other dinosaurs. However, using a new analysis of forelimb structure, the index of forelimb proportions, it was demonstrated that *I. mantelli* retained some characteristics associated with quadrupedality. Therefore, *I. mantelli* spent considerable periods of time walking or running bipedally; however it was not a bipedal as were the anatomically similar hadrosaurs, since its forelimb was well-adapted for locomotion. A reconstruction of an individual of this species in normal walking posture has been attempted (fig. 83).

***I. bernissartensis*.**

The considerably greater size attained by this species appears to have imposed some modifications in the forelimb construction. The manus, although similar in overall shape and functional abilities, is considerably more robustly constructed, to ensure a greater load bearing capacity for digits II, III and IV than was possible in *I. mantelli*. Comparisons with the forelimbs of *Anatosaurus* and *Tenontosaurus* suggest a close similarity with that of *Tenontosaurus*, a probable quadruped; this is further emphasised by comparing forelimb : hindlimb ratios, and the index of forelimb proportions with a variety of bipedal and quadrupedal forms. The results all suggest that this species was most probably a quadruped. *I. bernissartensis* spent most of its time in a quadrupedal posture; however, the possession of a prehensile fifth digit, and a very large ungual spur indicate that this species was capable of a bipedal gait; this was probably for grasping vegetation while feeding and for defending itself against large predators, in which case the added height gained by

swinging the body upwards may have been advantageous. A reconstruction of the probable normal walking posture of this species has been attempted (fig. 84); an indication of the probable range of movement of the forelimb has been included.

Growth : the limbs of *I. bernissartensis*.

The fortuitous discovery of a large number of moderately well-preserved, articulated skeletons of *Iguanodon* at Bernissart has long invited an investigation to assess growth characteristics and variability in this species. There are however a number of problems associated with these dinosaurs which have made estimations of growth in this species problematical. The condition of preservation of many of the skeletons is rather poor; this has created problems when trying to measure accurately the lengths of various limb bones. In addition, the majority of the specimens are apparently fully grown; only three specimens (IRSNB. 1726, 1729, 1730) are of an intermediate size and all of these are rather poorly preserved.

In spite of these problems, it has been possible to get at least an idea of growth trends in the limbs of this species. Only the most crude methods of analysis have been used to demonstrate the changes of limb proportions with growth, as befits the paucity and poor quality of the available material.

The proportional lengths of the limbs have been compared in two ways (table III). Firstly, the forelimb : hindlimb ratios have been calculated and expressed as a percentage. (The effective length of forelimb and hindlimb is considered to be : humerus + radius + metacarpal III and femur + tibia + metatarsal III respectively). Secondly, the percentage length of the various forelimb bones relative to the femur have been calculated.

From the admittedly imperfect results tabulated above, a few generalisations can be made. Adult (full-

TABLE II.

	Fem	Tib.	Mt. III	Hum	Rad	Mc. III
<i>I. bernissartensis</i>						
IRSNB 1534	102	89	35	85	54	20 ⁽¹⁾
IRSNB 1729	95	86	29	64 ⁽²⁾	47	17
IRSNB 1730	87 ⁽³⁾	78 ⁽⁴⁾	27	54 ⁽⁵⁾	—	14.5
IRSNB 1726	84 ⁽⁶⁾	74	27 ⁽⁷⁾	56 ⁽⁸⁾	40 ⁽⁹⁾	—
<i>I. mantelli</i>						
BMNH. R. 5764	67	62	23	38.5	26.5	12

(All lengths measured in centimetres and accurate to nearest 0.5 cm.)

N.B.

Several values for the lengths of the limb bones of these obviously crucial specimens are estimates based on the preserved part or parts of these elements. The procedures whereby these values have been calculated are indicated below.

(¹) This bone is partly restored with « carton-pierre »; its most probable length is indicated and coincides with that of metacarpal III of IRSNB. 1536, an animal commensurate with IRSNB. 1534.

(²) The distal condyles of this bone have been fractured and displaced; an estimate of its length has been made by simply allowing for displacement.

(³) (⁴) (⁵) The femur (fig. 85 B), tibia and humerus (fig. 85 A) of this specimen have been fractured in several places. In each case these bones have been reconstructed and their lengths estimated accordingly.

(⁶) A section of this femur is missing. The length of this bone has been calculated by summing and averaging the values of femur : tibia length for all specimens (1.13) and multiplying the length of the tibia of IRSNB. 1726 by this factor. The femoro-tibial proportions remain constant over a considerable size range and for several species of the genus *Iguanodon*; this procedure thus seems reasonably justified.

(⁷) The length of this metatarsal has been estimated from that of IRSNB. 1730 (27 cms), an approximately commensurate individual.

(⁸) (⁹) The humerus and radius of this specimen are fractured in several places, their lengths have been estimated after reconstructing each bone.

sized) individuals of *I. bernissartensis* have a relatively high forelimb : hindlimb ratio (~ 70 %). By contrast, the juvenile (intermediate-sized) individuals show a significantly lower ratio (~ 60 %). Broadly similar trends can be discerned when the individual bones of the forelimb are compared; however the humerus

appears to be the segment mostly responsible for the overall change in forelimb proportions (decreasing from 82 % of the length of the femur in the adult, to 62-68 % in the juveniles). Data from the well-preserved gracile species *I. mantelli* gives a forelimb : hindlimb ratio of 50 % and a humerus : femur ratio of 57 %.

TABLE III.

	fore : hind	Hum : Fem	Rad : Fem	Mc III : Fem
<i>I. bernissartensis</i>				
IRSNB 1534	70 %	82 %	53 %	19.6 %
IRSNB 1729	61 %	68 %	49.5 %	18 %
IRSNB 1730	(57 %)	62 %	(~ 48 %)	16.6 %
IRSNB 1726	(57 %)	67 %	47 %	(~ 17 %)
<i>I. mantelli</i>				
BMNH. R. 5764	50.7 %	57.5 %	38 %	18 %

N.B.

IRSNB. 1730 — Bracketed values are based on an estimated radius length of 42 cms.

IRSNB. 1726 — Bracketed values are based on the length of metacarpal III of IRSNB. 1730, i.e. 14.5 cm.

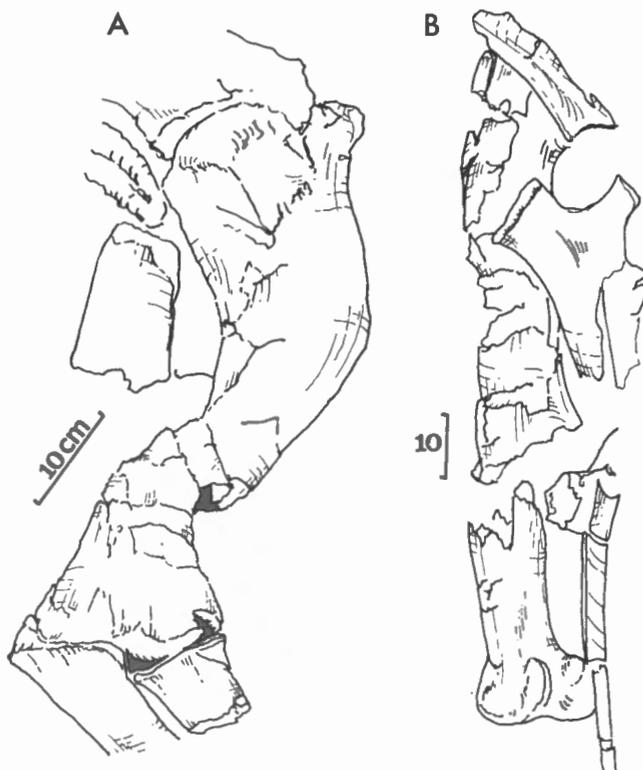


FIG. 85. — *Iguanodon bernissartensis*. (IRSNB. 1750).
A : the humerus; B : the femur; as preserved.

Therefore it appears that juvenile individuals of *I. bernissartensis* have limb proportions which are intermediate between those of adults of this species and apparently adult specimens of *I. mantelli*. The implications of these results lead to some novel suggestions concerning the mode of life of *I. bernissartensis* during ontogeny.

The approximate value of 60 % for the forelimb : hindlimb length in juvenile *I. bernissartensis* can be converted to a hindlimb : forelimb ratio of 1.6 - 1.7; this value lies within that of several hadrosaurs (fig. 82; tab. I) although it is less than that for *I. mantelli* (1.97) and for some hadrosaurs, e.g. *Anatosaurus*, 1.94. Judged by limb proportion data it would seem that juvenile *I. bernissartensis* had a mode of life comparable to that of hadrosaurs and *I. mantelli*; that is, they were only facultative quadrupeds, while adults with a hindlimb : forelimb ratio of 1.43 were facultative bipeds. Thus a possibly unique ontogenetic change seems to take place in the mode of life of *I. bernissartensis*. Juveniles have a predominantly bipedal mode of life while the adults are essentially quadrupedal.

At least two factors may have individually, or in combination, contributed to this phenomenon. Firstly, predation by what appear to have been relatively agile carnosaurus (*Megalosaurus*) may have been greatest on juveniles : this might be expected since fully grown *I. bernissartensis* are much larger than *Megalosaurus* and therefore perhaps less susceptible to predation. Survival of the juveniles would be favoured by agility

and the ability to flee from predators rather than by active defence. In this respect juveniles of *I. bernissartensis*, by adopting a mode of life comparable to *I. mantelli*, appear to parallel the strategy of avoidance probably used by the approximately commensurate adults of this species. Secondly, the adoption of an essentially quadrupedal way of life upon the attainment of full size may (also) have been a consequence simply of « dinosaurian » size in this species, i.e. the hindlimbs became unable to continually support the entire body weight once a critical body size had been reached and were, thereafter, augmented by the forelimbs.

It might be suggested that the hadrosaurs, which are the only other ornithopods of comparable size, remained bipedal as adults even though they were as large or larger than *I. bernissartensis*. However it seems that in hadrosaurs, the anatomy and physiology of the hindlimb and pelvis were such that they were better adapted for supporting the entire body weight. Although perhaps rather abstract, this explanation gains some support from the larger size of the sacrum in hadrosaurs (typically nine vertebrae; LULL and WRIGHT, 1942) and the straighter shaft of the femur; both are features which can be correlated with improving the weight supporting ability of hindlimb and pelvis.

Whatever the correct explanation might be for the unusual growth characteristics in the forelimb of *I. bernissartensis*, it is obvious that new, better-preserved material is required for a more precise analysis of growth changes in this species.

Individual variation and sexual dimorphism.

There appears to be relatively little individual variation exhibited by *I. bernissartensis*. In the skull, the only significant variation seems to be in the number of vertical tooth rows in the jaw, the maximum number which have been found are 29 maxillary rows and 25 dentary rows (IRSNB. 1536). There is rather tenuous evidence of variation in the degree of fusion of the exoccipitals with the surrounding occipital bones.

In the postcranial skeleton there are interesting changes in the proportions of the forelimbs, but these are linked to growth. There is occasional variation in the number of sacral vertebrae caused by incorporation of the first caudal vertebra (IRSNB. 1535). The fourth phalanx of digit V of the manus has variable form, from cone-shaped to that of a flattened disc.

Despite a thorough survey of the numerous Bernissart specimens, it has not proved possible to identify good osteological criteria for determining sexual morpho-types of *I. bernissartensis*. The long-held belief that *I. bernissartensis* and *I. mantelli* are sexual forms of a single species — dating from VAN BENEDEN (1881) and NOPSCA (1929) — is unfounded. Osteologically, these two forms appear to be perfectly distinct and valid species.



SUMMARY

The osteology of the skull of *I. bernissartensis* has been described as far as is presently possible; some regions of the skull, notably the braincase and palate, are known only in superficial detail and await the discovery of better preserved specimens. Neither the stapes nor the sclerotic plates have so far been found. The postcranial skeleton is by contrast reasonably well represented so that relatively few elements remain to be described.

Proatlases have not so far been discovered and this is probably related to the method of excavating the skeletons, whereby the skull, in each instance, was separated from the neck at an early stage of excavation. There are two phalanges in digit I of the manus and the metacarpal is fused with the wrist bones. Digits II and III bear large, twisted, hoof-like unguals; there are two phalanges in digit IV and four phalanges in digit V. The carpals are co-ossified and further reinforced by ossified ligaments. An « intersternal ossification » is found between the coracoids and sternal bones at the centre of the chest. The upper part of the sacrum, the sacral yoke and the internal surface of the ilium are poorly preserved. Three distal tarsals have been identified.

There is no strong evidence to suggest that *Iguanodon* possessed an elongate prehensile tongue; indeed indirect evidence of the form and function of the horny beak suggests that feeding was achieved by the beak rather than a prehensile tongue. The probable function of the beak of hadrosaurs is briefly reviewed; the evidence available favours a terrestrial foraging function rather than an aquatic filter-feeding function. The supraorbital bones are double, and not single elements which have undergone *post-mortem* fracturing as has been suggested in the past; their large size and prominent position above the orbit may indicate that they were used either for display or for protection of the eye. The construction of the occiput is reviewed and compared to that of related ornithopods; the apparent hypertrophy of the exoccipitals in more advanced forms is tentatively correlated with progressive improvements in the masticatory abilities of the more advanced ornithopods (iguanodontoids, hadrosaurs). A pair of post-temporal openings are present in the occiput, the *vena capitis dorsalis* passed through these openings and

opens out in the temporal cavity against the outer wall of the braincase.

The posture of *I. bernissartensis* has been re-assessed and it is concluded that the vertebral column of this species was normally held in a more horizontal attitude. The slender pubic peduncle of the ilium — to paraphrase GALTON (1970) — was reinforced by the massive first sacral rib, has a well-developed acetabular surface and is well able to withstand the thrust from the head of the femur; thus an *exclusively* horizontal posture for this species is unwarranted. In view of this change of posture, the function of the forelimb has been re-analysed, using a variety of methods, in *I. bernissartensis* and the contemporary gracile species *I. mantelli*. It is concluded that the forelimb in both species was suitable for use as a walking limb. The manus shows a remarkable degree of functional differentiation of the digits so that the manus can be used for weight support, as a defensive weapon and for grasping. *I. bernissartensis* the larger and more robustly constructed of these two species appears, from its limb proportions, to have been primarily quadrupedal, while the gracile *I. mantelli* was primarily bipedal. The relatively greater size of the pollex spine of *I. bernissartensis* compared to that of *I. mantelli* may be a reflection of the difference in mode of life in these species: the former, being less agile, used the pollex as a defensive weapon against predators, while the gracile species used agility and speed to avoid predators.

A study of growth trends in the limbs of *I. bernissartensis* reveals that juveniles have disproportionately short forelimbs. The ratio of hindlimb:forelimb for these juveniles is more similar to that of *I. mantelli* and hadrosaurs rather than that of adults of this species, which in turn suggests that juvenile *I. bernissartensis* were primarily bipedal, while adults were quadrupedal. The possible reasons for this ontogenetic phenomenon are discussed and it is tentatively suggested that it was related to natural selection for large size in this species (to combat predation) and the physical problems of this large size.

Variation and sex dimorphism in *I. bernissartensis* are briefly reviewed. This species exhibits relatively little individual variation and no sexual morphotypes can be distinguished.